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A CARBON-NITROGEN MODEL OF A PINE FOREST SOIL ECOSYSTEM - A DEVELOPMENT PAPER

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A CARBON-NITROGEN MODEL OF A PINE FOREST SOIL ECOSYSTEM - A DEVELOPMENT PAPER

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Abstract

A carbon-nitrogen model has been constructed for some soil processes taking place in the FH-layer of a pine forest. It includes processes as decomposition, respiration, mineralisation, immobilisation and decomposers biomass formation. Most of the data used to construct the model was taken from the literature and a few from own measurements. A number of runs have been carried out. One of them is defined as the standard run. The other deal with the sensitivity of the model to changes in chosen parameter and to changes in structure. Mineralisation, in particular, shows to be very sensitive to changes in parameters describing the kinetics of decomposers' growth and to changes in the model structure.

1. Introduction

The study of soil processes in the project has been formalised in a soil nutrient model (named the N-model - present generation designated N 1). The overall aim of the model is to describe the competition for nitrogen (other nutrients are of secondary priority) between roots, microorganisms, and soil (absorption) in an undisturbed forest soil ecosystem. For practical reasons, the model has been divided into an organic (N1ORG) and an inorganic (N1ING) submodel. This development paper deals with the organic submodel (N1ORG).

Several attempts have been made at constructing simulation models of the decomposition process. Many difficulties arise when, for example, the decomposition processes, biomass formation and nitrogen mineralisation are to be organized in a simulation model. One requirement is that the model should have biological significance, and another is that data obtained should fit into it. Lack of suitable data often limits the possibilities of constructing and validating a model. For example, the processes of decomposition, mineralisation, biomass formation as well as the respective compartments often have to be studied on a small test site and a high degree of organisation in the studies is needed.

Many investigations have been carried out on decomposition determined as weight loss. Less work has been done taking into account the actual changes taking place in the substrate during decomposition. It is well known, though, that the C/N quotient in substrates with little nitrogen decreases during the decomposition process (Smith & Douglas, 1971; Berg, to be published). The inorganic nitrogen formed is believed to be immobilised during the microbial breakdown of the substrate. The nitrogen is thus largely recycled in the substrate while carbon is released in the form of CO_2. The measured increasing percentage of nitrogen could be due to the presence of microorganisms and the substrate itself could have a lower rate of increase in the C/N quotient (Harmsen & Kohlenbrander, 1965).

The present paper is intended to be a presentation of the state of the work and may be regarded as a working document for the present refinements of the model. It is intended that this paper should be followed by more complete descriptions as improvements and refinements are worked out.

2. Objectives

The objective of the organic part of the soil nutrient model (N1ORG) are to describe the mineralisation and immobilisation of nitrogen with the time resolution of one day. The nitrogen mineralisation is an input to the inorganic part of the model (N1ING).

The model presented is modified from a submodel of decomposition developed in the US Desert Biome (Parnas & Redford, 1974). Although originally developed for a desert, its general applicability is such that it was possible to validate it with data from the Norwegian IBP Tundra Biome studies. These data are quite different from those by which the model was constructed, but nevertheless gave acceptable results (Wielgolaski, Redford & Valentine, 1974).

Our first aim is to make the presented model work properly with available data from the FH-layer in a 120-year-old pine stand (Ih VA at Ivantjärnsheden). The soil is divided into three layers viz., the S-layer, a combined FH-layer, and the mineral soil down to 20 cm depth. The three layers behave differently in many respects. We preferred, however to work with one soil layer in a first attempt to make the model work. A number of runs were carried out with the four available data of our own. It is our intention to run the three soil layers in a forthcoming N 1 model. This will be built around a number of modules. The present N1ORG model constitutes the basis for the organic module of N 1.

3. Verbal and graphical description of the model

For each soil layer, a number of different structures can be chosen to build the model N1ORG (see section 5). In our runs with the FH-layer we have been particulary interested in two of these structures and they are shown in figures 1-a and 1-b. With the structure shown in figure 1-a three separate decomposing substrates (organic materials is used sometimes in this paper as synonymous) are present in the layer, i.e. litter (L), dead organisms (DO) and humus (H). The second structure with only two substrates is shown in figure 1-b. Here, humus and dead organisms have been combined in one decomposing substrate that we have called, provisoriously, soil organic matter (SOM or S) (see 4.5). Regardless of the structure, for each substrate three compartments (state variables) are defined (see 4.2): Y(1) is protein carbon, Y(2) is other carbon and Y(3) is protein nitrogen in the substrate. Compartments X02,(decomposers biomass) and X01, (inorganic nitrogen in the soil) are common to the soil layer and independent of substrate concentrations. Inorganic nitrogen, (X01), can be present partially in soil water phase and partially adsorbed to soil particles. These amounts are represented by functions G1 and G52 respectively (see 4.12 and 5.1.1).

At each time interval (1 day in the model) the processes shown in figures 1-a and 1-b will modify the values taken by the compartments at the beginning of such time interval. An enlargement of the processes accompanying the decomposition of a given substrate is given in figure 1-c. This figure shows in a clear way the processes associated to carbon and nitrogen dynamics. The rate of processes are represented by the G-functions showed and explained in the same figure. The nomenclature used in figure 1-c for the G-functions and for the substrate compartments is of a general nature and refers to any substrate at any soil layer. Further on, in order to refer to a given G-function or compartment for one particular substrate we shall add to the G or compartment symbol the capital letter representing the substrate. This means that G19L, G19DO and G19H, for example, will represent mineralisation from litter, dead organisms and humus respectively. In some cases and in order to simplify writing, the vectorial notations has also been used; in such a case, G19(m) will mean the mineralisation from substrate m. Once the rates for each substrate have been calculated the total rate for the soil layer can be calculated by adding the rates for each substrate. So, the total nitrogen mineralisation for the FH layer is represented by $G19T = G19L + G19DO + G19H$, or, in vectorial notation by: $G19T = \sum_{m=1}^{3} G19(m)$. The method of calculating the rate of processes for any substrate will be discussed below. However, two variables of interest must first be presented:

- the carbon-nitrogen ratio of the substrate, defined at each time t, as the sum of the carbon compartments, Y (1) and Y (2), divided by the organic nitrogen compartment Y (3) (see 4.2 and 5.1.4) and
- the critical carbon-nitrogen ratio, which does not depend on time t, and is defined as: average carbon fraction in decomposer cell divided by the product of average nitrogen fraction in decomposer cell and decomposer assimilation efficiency (see 5.1.6).

Since practically all processes shown in figure 1-c depend on G 13 (biomass formation) at each time t this process is calculated first. Some of the factors on which G 13 depends are: Y (1), Y (2), Y (3), NH_4^+, decomposer biomass, temperature, moisture and the optimal growth for the substrate. Thus, in order to calculate G 13, the temperature and moisture conditions at time t must first be defined. This is done by means of the driving functions (see 5.2). G 13 can be calculated as the "stationary growth" (Parnas, 1975a) or as the "mean growth" (Parnas, 1975b). In any run of the model, one of both alternatives must be chosen, and this is done by attaching a convenient value to one of the parameters of the model (see 5.1.10). Once G 13 has been calculated, the decomposer demand on carbon and nitrogen can be calculated as P018, G13 and P020, G13 respectively, where P018 and P020 are two parameters giving the carbon and nitrogen concentration in the decomposer cell (see fig. 1-c). The total carbon decomposition, G 14, is calculated by dividing this carbon demand by the assimilation efficiency (5.1.12). On the other hand, G 14 minus the carbon demand gives the respiration rate, G 17 (5.1.16).

Nitrogen fixation, G 23 is calculated by multiplying the nitrogen demand by the fraction of decomposer biomass which fixes nitrogen (5.1.13). The amount provided by G 23 is then subtracted from the total nitrogen demand; the remaining amount is multiplied by the inorganic nitrogen fraction, $NH_4^+/(Y\ (3) + NH_4^+)$, and in this way immobilisation, G 20, is calculated (5.1.19). The sum of G 20 and G 23 is subtracted from the total nitrogen demand and in this way we obtain the amount of nitrogen demand provided by Y (3), i.e., the organic nitrogen demand (arrow without number in fig. 1-c).

We then calculate the protein-carbon decomposition. This is done as follows (5.1.14):

- if the carbon-nitrogen ratio of the substrate is greater than the critical carbon-nitrogen ratio, G 15 equals the organic nitrogen demand times the carbon-nitrogen ratio of the protein.

- if the opposite happens, G 15 is calculated as G 14 times the protein--carbon fraction, Y (1)/(Y (1) + Y (2)).

Other carbon decomposition is calculated as G 14 minus G 15 (5.1.15). Protein-nitrogen decomposition, G 18, is calculated as G 15 divided by the carbon-nitrogen ratio of the protein (5.1.17). Mineralisation, G 19, is calculated by subtracting the organic nitrogen demand from G 18. It can be seen that if protein-carbon has decomposed according to the first way defined above, G 19 will equal zero.

The remaining processes shown in fig. 1-c are formulated in a very simplified way by the model (see 4.11 and 5.1.11 for mortality, G12; 4.7.3 and 5.1.23 for external breakdown, G39, and 5.1.25 for nitrogen uptake by roots, G70). Regarding the inputs also shown in the figure, they clearly depend on the substrate in consideration (see figs 1-a and 1-b). If the substrate is litter, the inputs will represent the different chemical fractions in litter formation, a driving function (see 5.2). If the substrate is DO (dead organisms), the inputs are given by G12, mortality, times the fraction of the given chemical compound in the decomposer biomass, plus the amount coming from other soil layers (see 4.6 and 5.1.24). In case the substrate is humus, the inputs will represent external breakdown coming from litter and dead organisms. Finally, if the substrate is SOM (soil organic matter), inputs will represent mortality plus transport plus breakdown (see 4.5 and 5).

4. General assumptions and definitions

In order to formulate the mathematical descriptions for the processes it was necessary to make a number of assumptions for formulating equations of the processes. One assumption is that the litter or organic matter being decomposed is homogeneous. More specific are the following assumptions/ simplifications taken from Parnas (1975a).

- Carbon loss from the organic substance under decomposition is proportional to the growth rate and requirements for maintenance energy for the microorganisms decomposing it.

- The growth rate of the microorganisms under certain specific environmental conditions (temperature, moisture, pH, etc.) and a given type of litter or other organic substance increase with increasing carbon and nitrogen concentrations.

- The decomposing microorganisms use the nitrogen compounds as nitrogen sources according to their relative availability.

- The release of nitrogen from carbon-nitrogen compounds (C-N compounds) in the organic substance under decomposition is proportional to the loss of carbon from the same C-N compounds.

- As energy and carbon source, the decomposing microorganisms can use carbon bound or not bound to nitrogen.

4.1 The soil layer (FH-layer)

The FH-layer extends from the S-layer down to the middle of the bleach soil. The only litter appearing in this layer is root litter; and the amount is given in Table 1 (Persson, pers. comm.). There is an input of solid material from the S-layer consisting of humus and dead organisms. The thickness of the layer varies at the site studied, but this variation is not considered here. The amount of soil organic matter was estimated at 1300 g m^{-2} (Staaf & Berg, 1976). Charcoal from a forest fire was found at the site but is neglected here.

4.2 Substrate quality in the model and C/N quotients

The substrates consist of various chemical components in differing amounts. It is believed that these have different rates of degradation and it seems that lignin is degraded more slowly than cellulose and hemicelluloses, which are degraded more slowly than water soluble substances (Berg, to be published). In the NICRG model the substrate quality is so far used in the following way: The model subdivides each of the substrates viz.,

- Litter, dead organisms and humus into three subgroups on a chemical basis. The easily available carbon viz., that in proteins and nucleic acids, makes up the Y(1)-compartment. It is defined as "the amount of carbon bound to nitrogen".

- Carbon compounds not containing nitrogen, like cellulose and hemicellulose and - so far - C in lignin (in spite of "lignin nitrogen"), constitute the subcompartment Y (2).

- The third compartment Y (3) contains the amount of nitrogen bound to carbon viz., the amount bound to proteins and nucleic acids. These C and N compounds are used to define a C/N ratio only taking into account the protein-nitrogen of the substrate as nitrogen source. The quotient is referred to as C/N_1. Since the N_1-nitrogen cannot be measured in substrates where microorganisms are present, it must be calculated. In the model outputs we can obtain control values where the actually measured C/N is given. This quotient is referred to as measured C/N and corresponds to the traditionally used C/N quotient which includes microorganisms.

The reason for this subdivision and the special C/N_1-quotient is the different conditions for mineralisation of nitrogen and the utilisation of carbon. It is uncertain whether this subdivision is the best one for our system, and work is being carried out on the possibility of including another compartment for nitrogen viz. lignin-bound nitrogen. There is now no difference between e.g. lignin and hemicelluloses in decomposition rate in the model and all substances classified as Y(2)-compounds in litter have the same decomposition rate.

4.3 Litter

Litter is found in the three soil layers but its components vary according to the layer.

The FH-layer litter is made up of root litter exclusively viz., heather roots, pine roots and lingonberry roots. These litter components, as well as those in the S-layer, have different decomposition rates. The different rates depend on the type of litter and the diameter of the roots, e.g. pine root litter is decomposed twice as fast as heather roots, and litter of 3 mm diameter about twice as fast as that of 6 mm (Berg, to be published). An average decomposition rate is used in the model.

4.3.1 Litter inputs

There are very specific abiotic factors, such as temperature and moisture, that govern the formation of litter. However, owing to lack of information, it has so far been necessary in the model to give the litter inputs at selected times of the year independent of abiotic factors.

The litter input to the FH-layer consists only of root litter, viz., pine roots of diameters less than 5 mm, heather and lingonberry roots. The present assumption is that two litter inputs equal in size take place annually, during November and April.

4.4 Input of solid organic material from the S-layer

The litter that falls on the S-layer or is formed there is decomposed to such an extent that it is transformed into soil organic matter (SOM) or humus already in the S-layer (Staaf & Berg, in manuscript). This means that the lowest part of the S-layer is made up of SOM and the input to the FH-layer thus becomes either SOM or humus and dead organisms (see the discussion in section 4.5 "SOM versus humus and dead organisms").

The mechanisms for downward transport of litter through the moss/lichen layer are not known. The transport may, for example, be influenced by the snow, pressing down the litter particles in the upper parts of the moss layer. Moss growth may also have an effect. As the mosses grow, the needles descend in the profile in their original position. For the purpose of the model we have made the following approximation of the transport: the SOM (humus and dead organisms) are transported at a constant rate during the time when temperature of the layer is above $0^{o}C$.

The transport time through the S-layer determines the amount of carbon that enters the FH-layer owing to the release of CO_2. The nitrogen is not dependent on transport time since it appears that none or very little nitrogen is given off from the litter particles during breakdown (Berg, to be published).

Measurements and calculations of times for the downward transport of needle litter through the S-layer gave a rough figure of 5-6 years (Berg 1974; Berg, in manuscript) at which the litter might be decomposed by about 90%. Using a value of 200 $g \cdot m^{-2} \cdot yr^{-1}$ litter input to the S-layer (Flower-Ellis, pers. comm.) we would thus obtain 20 $g \cdot m^{-2} \cdot yr^{-1}$ of input to the FH-layer. This quantity of 20 g thus retains all the nitrogen present in the original 200 g of litter (0.4%).

4.5 Soil organic matter (SOM) versus humus and dead organisms

Litter under decomposition finally reaches a stage where it can no longer be described as litter. At this stage the word *humus* is applicable only as unidentifiable substances remain. The term *soil organic matter* (SOM) is as applicable and has been used much in modelling work to designate the structurally amorphous mass of humus, among other things, without specifying what is included. The SOM includes humic substances, litter remains, and dead microorganisms. Considering the average amounts of living microorganisms and their high nitrogen content, their weight and amount of nitrogen are sometimes subtracted when calculating the amount of SOM. There are different ways of regarding the visually unidentifiable organic substance present in the FH-layer. It can be regarded as a rather homogeneous mass or as consisting of different components. In the present work and in the N1ORG modelling we chose to distinguish carefully between what we call soil organic matter and what we call humus. Among the reasons for this are different approaches to the nitrogen mineralisation. The meanings of the different terminologies used here are discussed below. The model was run with the two following approaches:

- As soil organic matter
  Soil organic matter is taken to mean the amorphous substance including the nonidentifiable humus substance and dead organisms. The figure for the living organisms - in reality the fungal and bacterial biomasses - has been subtracted. In this case the SOM contains protein-nitrogen and protein-carbon as well as "other carbon". The SOM has a C/N quotient of about 50 (Staaf & Berg, in manuscript).

- As humus and dead organisms
  In this case the amount of dead organisms in the SOM is calculated and subtracted. We thus obtain two very different substances. The humus contains no easily degradable carbon-nitrogen compounds and the protein-nitrogen subcompartment is therefore set at a low value and so is the amount of protein-carbon. The "other" carbon subcompartment has a rather high value, and the humus compartment thus has a very high value for the C / N_1 quotient. The slowly available nitrogen in the humus has not been taken into account so far.

In the dead organisms compartment the C / N_1 quotient is 11.3 (Söderström, pers. comm.).

4.6 Nitrogen inputs

The main nitrogen input appears to come with the litter formation (see 4.3.1) and might be $0.46 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

The other large nitrogen input probably takes place via the transport of SOM (or dead organisms) and is thus protein nitrogen from the S-layer. This input, which might reach an order of magnitude of $0.1 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, is discussed in section 4.4.

The nitrogen fixation in the FH-layer is very small, probably of an order of magnitude of 0.01 $g \cdot m^{-2} \cdot yr^{-1}$ (Granhall, pers. comm.). It has been included in the model, however, and it is assumed that the nitrogen fixation is carried out by 2% of the biomass. The nitrogen fixation has the same temperature and moisture dependence as growth and decomposition processes.

Dry and wet deposited N (NH_4^+) goes to the S-layer and is assumed to be further transported by water or taken up by the decomposer organisms and the vegetation. It has thus been incorporated in other processes, and is not a separate process in the present model. The faeces fall is rather small but might be included in the model later on. No denitrification appears to be taking place at the site and the process has thus not been included in the model.

4.7 Decomposition

General

The decomposition process depends, among other factors, on temperature, moisture, amount of decomposer organisms and substrate quality, the latter including factors like percentages of lignin and nitrogen. The type of substrate, such as humus, dead organisms and various types of litters, also has a high influence. The position in the soil profile determines the amount of oxygen and carbon dioxide available, which both affect the decomposition rate.

The temperature and moisture influences are at present represented in the model by carbon functions (see sections 5.1.7 and 5.1.8), which will be modified in the light of field measurements.

4.7.1 Decomposition of litter

Only root litter is present in the FH-layer and both the origin and the diameter of the root litter affect its decomposition. Thus, the *Calluna vulgaris* are decomposed at about half the rate of *Pinus silvestris* roots (Berg 1977, in manuscript). Lingonberry roots and pine roots are for the purpose of the model assumed to have about the same decomposition rate. At present the overall decomposition rate is approximated to 40% per year.

During the decomposition of a certain litter type the C/N quotients decrease from about 100 commonly found in the roots down to, perhaps, 50 as is found in the SOM (Staaf & Berg, in manuscript). This is due to the recycling of nitrogen in the sample, carried out by the microorganisms and the release of carbon as CO_2. The decomposition of a certain litter type thus starts initially at a high value of the C/N quotient, with nitrogen limiting.

Under the conditions prevailing at Ivantjärnsheden, nitrogen is probably the limiting factor in all stages of decomposition. The C/N_1 quotient is used for the regulation mechanism. It has a higher numerical value (about 90) than the C/N quotient.

4.7.2 Decomposition of SOM or humus and dead organisms

In the SOM the presence of proteins and certain parts of microbial litter give rise to a pool of easily degradable C-N compounds which are well mixed with less degradable substances like lignin and humus. The C/N quotient of the SOM as a whole is relatively constant and has been measured as varying around 50 (Staaf & Berg, in manuscript).

When we regard the SOM as consisting of the separate substances, humus and dead organisms, the conditions for the compartments become different. Dead organisms have Y(1)- and Y(2)-carbon as well as Y(3)-nitrogen and a C/N_1 quotient of 10-12. Humus contains almost only Y(2)-carbon and it is assumed that the amounts of protein-carbon and -nitrogen available are low. In the model they are given a low value which might be realistic and the resulting C/N_1 quotient does not allow of any mineralisation.

4.7.3 External breakdown

In the breakdown of litter there will always be particles left which can no longer be called litter but are termed humus (see section 4.5). We do not know at what level of decomposition a litter particle - a needle, say - will turn into nonidentifiable humus particles. The process is expressed as a fraction of the decomposition and is at present assumed to be 10%.

4.8 Carbon mineralisation (respiration)

The carbon mineralised in the model is regarded as a fraction of the amount of carbon being decomposed. The fraction corresponds to the complement of the efficiency. If we write the efficiency as:

$\frac{\text{C used for growth}}{\text{C total decomposed}}$, the fraction thus is $1 - \frac{\text{C used for growth}}{\text{C decomposed}}$

There are many values suggested for the efficiency factors for microorganisms and values between 5% and 30% are given in the literature. According to Söderström (pers. comm.) a value of 10% could be expected for fungi, and has been used here mainly because the fungal biomass predominates (Bringmark *et al.*, 1975).

4.9 Decomposer biomass

The biomass of the FH-layer at the test site is made up of microorganisms and soil animals, the latter with Acari and Cryptostigmata dominating in biomass, each varying between 300 and 20 µg/g soil. The microbial biomass, - fungi and bacteria - is dominated by the fungi (Bringmark *et al.* 1975). The fungal biomass as calculated by the Jones-Mollison technique (Jones & Mollison, 1948) varies between 6 and 24 $\text{mg}\cdot\text{g}^{-1}$ of FH-layer and with 1300 g of SOM we have 7-28 $\text{g}\cdot\text{m}^{-2}$. The living fungi appear to make up about only 10% of this amount (Söderström, pers. comm.).

The biomass so far considered in the model is only the quantitatively dominating fungal one. The biomass variation is regulated by the growth and mortality functions. The whole biomass is considered to have a decomposing function in the system.

4.10 Formation of decomposer biomass

The growth rate of the microbial biomass is a function of the concentration of carbon and protein nitrogen and the microbial biomass. An any selected amount of microbial biomass and excess of carbon and nitrogen, the population will grow at a maximum rate. There is a dependence on temperature and moisture. At present these relationships are simple. See section 5.1.7 and 5.1.8.

4.10.1 Kinetics for substrate dependence

At present two ways of expressing mathematically the kinetics of growth are used (see 5.1.10):

- the Michaelis-Menten equation
- the function for mean growth

Both of these functions have been used by Parnas (1975a, 1975b) and the latter is a simplified version without the Michaelis-Menten parameters for carbon and nitrogen utilisation. Both approches modify the value for maximum decomposer growth as environmentally adjusted

(5.1.9). They further take into consideration biomass and amounts of carbon and nitrogen available for decomposition.

4.11 Mortality

Proper description of the mortality process in a model is not possible at present owing to lack of knowledge and the following simplification is thus made: The microbial population has a constant average death rate under normal conditions (when an energy source is available). Thus, in normal conditions, death and growth occur simultaneously, and the net change in biomass depends on the relative magnitude of these two processes. When the populations are starved of energy - that is, carbon - the mortality constant increases and at the same time no growth occurs.

4.12 Total nitrogen in soil water

The total amount of nitrogen dissolved in soil water equals the amount of inorganic nitrogen dissolved viz. $NH_4^+ + NO_3^-$, since the amount of organic N-compounds in solution is negligible (Bringmark & Petersson, 1975).

The soil-water nitrogen varies considerably in amount from time to time depending, among other factors, on moisture conditions.

In this model the soil water nitrogen is represented by the function G1, which in model N1 will be provided by module INORG. A very brief discussion follows here since details can be found in the forthcoming N1ING report.

The ionic concentrations can be determined for the soil system by assuming chemical equilibrium between the soil solution and the adsorbed phase. In this way, the amount of every ion (e.g., NH_4^+) in soil water, will depend on the instantaneous state of the soil complex.

There is a simpler, but only approximate, method of doing this. The variations in soil-water concentration for a given ion can be determined starting from variations in the total soil concentration (e.g. as produced by mineralisation) by means of the soil buffer capacity. The soil buffer capacity for a given ion can in turn be determined from the adsorption isotherm for the ion.

Work is currently in progress to obtain this kind of information concerning NH_4^+ and other ions. N1ORG simply assumes that all NH_4^+ in the model is in the soil-water phase (i.e. buffer capacity equal to unity and adsorbed amount equal to zero).

4.13 Nitrogen mineralisation

The transformation of organic nitrogen to ammonia takes place at a relatively low rate in the FH-layer at the Ivantjärnsheden site. The nitrification process has a rate much lower than that for formation of ammonia and denitrification does not take place at all.

4.14 Transport of dissolved substances

The amounts of carbon compounds and organic nitrogen transported between layers are negligible and are assumed to be equal to zero in the model. The NO_3^- and NH_4^+ transport between the different layers is also assumed to be equal to zero in this model. Leaching of inorganic nitrogen will be developed in the N1ING model.

4.15 Immobilisation of inorganic nitrogen

Immobilisation describes the rate at which inorganic nitrogen is transferred to microbial biomass. The immobilisation takes place only as a transfer from the soil-nitrogen compartment to the biomass compartment. It is assumed that the microorganisms can use organic and inorganic nitrogen equally well but at rates depending on their relative availability.

5. Mathematical description

According to one of the hypotheses of this model, organic materials with a higher C/N_1 ratio than the critical value do not contribute to nitrogen mineralisation. That means that, as far as nitrogen mineralisation is concerned, it is of no significance to have those materials as separate entities in the model or clustered together. Since the values of the parameters determining the critical C/N ratio are very uncertain, we have aimed at building a model with a rather flexible structure. Flexibility is a necessary condition if one wishes to test the significance of alternative structures in a model.

At its maximum capacity, N1ORG can manage, at the chosen soil level, five organic materials (substrates) and five boxes for each material. The chosen structure for a given run can be specified by giving convenient values to certain parameters (see Table 1). If the number of boxes for a given material is set equal to zero, N1ORG will cluster this material with SOM and the inputs corresponding to this material will correspondingly be attached to SOM.

In order to have the desired flexibility in structure, it has proved necessary to attach only one transfer to each box. Thus, the model connects box Xnn to the transfer T00nn which in that way actually becomes the time derivative of box Xnn. Each transfer (derivative) is defined as the algebraic sum of a series of processes which are represented by the auxiliary functions G. We can understand this if we look at Fig. 1. The time derivative of compartment NH_4^+, for example is calculated as

$T0001 = \sum_m (G19(m)-G20(m))-G70$ where the sum extends over all substrates m,

and in a similar way for the remaining compartments. This procedure is also convenient from the point of flexibility: processes can be changed by just redefining the corresponding G, or new processes can be included by just increasing the number of G-functions in the model. This has been the case with e.g. nitrogen fixation, nitrogen uptake by roots and transport between horizons which were not included at the preliminary version of the model.

Functions G1 to G49 are reserved for the organic modules ORG and DECERS, G50 to G69 for INORG and G70 and onward for the ROOT module. A list of G-functions for N1ORG is presented. The model needs some G-functions which should actually be calculated by some other module, e.g. G1 and G70. It should then be understood that these functions, as they are presented in N1ORG, are very provisory and simplified in character.

The modules (subroutines) around which N1ORG is built are:

- DECERS This subroutine calculates decomposers growth (biomass formation), mortality, etc.
- ORG Calculates decomposition, mineralisation, inputs to the substrates organic transports, etc.

The list of equations defining each G will now be written with the parameters corresponding to LITTER. It is clear that each time it is called, ORG fits the parameters according to the material under consideration. The same applies to compartments, i.e. they are fitted at each call of ORG; internally, ORG uses the five component vectors Y, with the following meaning: Y (1) protein-carbon for the given material, Y (2) other carbon, Y (3) protein nitrogen, Y (4) and Y (5) other possible chemical components for the given material.

The model produces a rather large amount of information and it is probably unnecessary to make a graph of each G-function. Even if all of them are actually available for plotting, we have made a selection of what we considered the most interesting information (see Legend to N1ORG graphs, p.46). The initial compartment values for a typical run are seen in Table 2 (only one soil level; in this case the FH-horizon).

5.1 Auxiliary variables

5.1.1 Inorganic nitrogen (NH_4^+) in soil water ($g \cdot m^{-2}$ soil)

The inorganic nitrogen in soil water is here represented by the function G1. As mentioned previously, we simply have:

G 1 = X01

where:

X01 is the total amount of inorganic nitrogen

5.1.2 Total nitrogen available to decomposers ($g \cdot m^{-2}$ soil)

G2L= Y3L + G1

where:

Y3L is the protein nitrogen in litter

5.1.3 Total carbon available to decomposers ($g \cdot m^{-2}$ soil)

G3L= Y1L + Y2L

where:

Y1L is the protein carbon in litter

Y2L is other carbon in litter

5.1.4 C/N, ratio in substrate

G4L = G3L/Y3L

5.1.5 Total carbon used by decomposers per unit biomass increment

G5 = P018/P019

where:

P018 is average carbon fraction in the decomposer

P019 is ratio of carbon assimilated to carbon decomposed (assimilation efficiency)

5.1.6 Critical carbon-nitrogen ratio

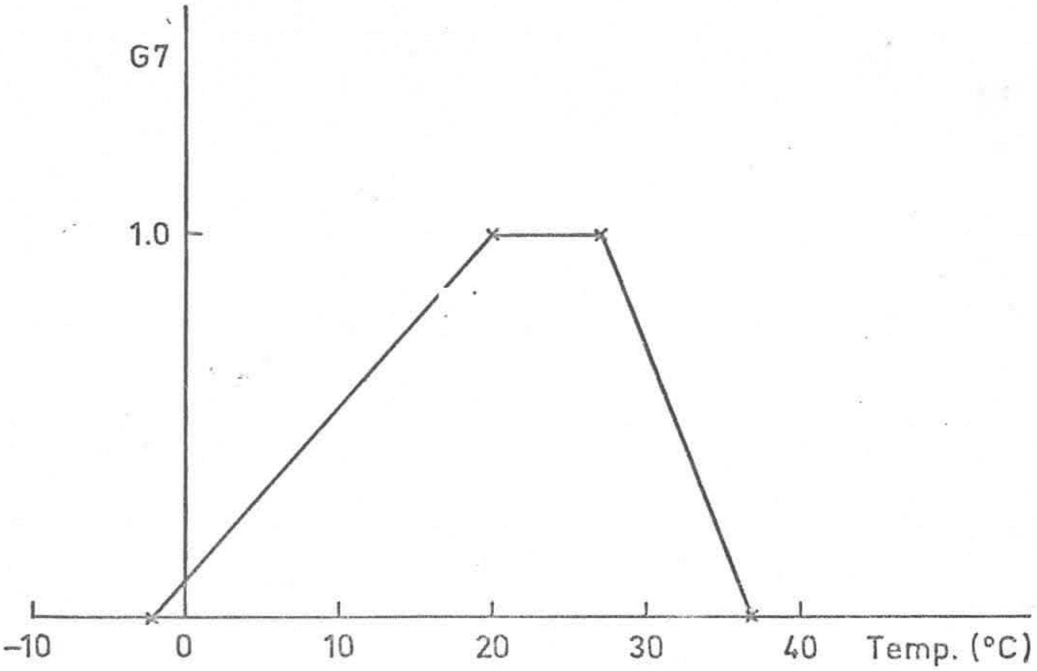
G6 = G5/P020

where:

P020 is average nitrogen fraction in the decomposer cell

5.1.7 Temperature scale factor for decomposer growth

It is given by function G7; to define this function, four parameters are required as shown in the figure and their values are given in table 1 (see P005, P006, P007 and P008).



5.1.8 Moisture scale factor for decomposer growth

G8 is given by the same kind of function as G7; the parameters in this case are: P009, P010, P011, P012.

5.1.9 Maximal decomposer growth rate environmentally adjusted (day^{-1})

G9L= P027 * G7 * G8

where:

P027 is maximal (optimal) growth in LITTER

5.1.10 Decomposer growth (g biomass$\cdot m^{-2} \cdot day^{-1}$)

There are at present two alternative ways of calculation included in N1ORG, and both of them are tested in different runs. If parameter P017 is set equal to zero, N1ORG will calculate growth according to Parnas, (1975a):

- Decomposer growth (stationary) (g biomass $\cdot$ m^{-2} $\cdot$ day^{-1})

  $G13L = G9L * G3L * G2L * X02 / [(P080+G3L) * (P085+G2L)]$

  where:

  P080 is the Michaelis-Menten constant for litter carbon utilisation
  P085 " " " " " " nitrogen "
  X02 is decomposer biomass (g biomass$\cdot m^2$)

  If parameter P017 is set equal to unity N1ORG will calculate growth according to Parnas (1975b):

- Decomposer growth (mean) g biomass$\cdot m^{-2} \cdot day^{-1}$)

  If G4L is greater than G6 the mean growth is calculated as:

  $G13L = (G2L+G3L) / [(G4L+1) * G22L * P020]$

  If G4 is less than G6 this growth is defined as:

  $G13L = (G2L+G3L) * G4L /[(G4L+1) * G22L * G5]$

  In these equation G22L is the growth time in litter (time taken for decomposers to reach the stationary phase) and is defined as:

  $$G22L = \ln \left[1 + \frac{(G2L+G3L)}{X02 * (G5+P020)}\right] / G9L \qquad \text{(days)}$$

5.1.11 Decomposer mortality (g biomass$\cdot m^{-2} \cdot day^{-1}$)

If there is carbon available in the system:

$G12 = P032 * X02$

where:

P032 is normal mortality rate

If there is no carbon available:

$G12 = P033 * X02$

where:

P033 is starvation mortality rate

Mortality must go as input to DO, if this substrate is present in the chosen structure for the run, otherwise to SOM. To do that, G12 is conveniently partitioned by the model into the different chemical components Y(1), Y(2) and Y(3).

5.1.12 Litter carbon decomposition (g·m^{-2}·day^{-1})
G14L = G5 * G13L

5.1.13 Nitrogen fixation (g·m^{-2}·day^{-1})
G23L= P021 * P020 * G13L
where:

P021 is the fraction of biomass X02 which fixes nitrogen

5.1.14 Protein-carbon decomposition (g·m^{-2}·day^{-1})
If G4L is greater than G6 we have:
G15L = (P034 * P020 * G13L* Y3L/G2L * (1 - P021)
where:

P034 is C/N ratio in proteins

If G4L is less than G6 we have:
G15L= G14L* Y1L/G3L

5.1.15 Other carbon decomposition (g·m^{-2}·day^{-1})
G16L= G14L- G15L

5.1.16 Respiration rate (g·m^{-2}·day^{-1})
G17L= (1 - P019) * G14L

5.1.17 Protein-nitrogen decompostion (g·m^{-2}·day^{-1})
G18L= G15L/ P034

5.1.18 Protein-nitrogen mineralisation (g·m^{-2}·day^{-1})
G19L= G18L- (P020 * G13L* Y3L/G2L) * (1 - P021)

5.1.19 Nitrogen immobilisation (g·m^{-2}·day^{-1})
G20L= (P020 * G13L* G1/G2L)* (1 - P021)

5.1.20 Protein nitrogen net mineralisation ($g \cdot m^{-2} \cdot day^{-1}$)
G21L= G19L- G20L

5.1.21 Total material ($g \cdot m^{-2}$)
G30L = Y1L + Y2L + Y3L + Y4L + Y5L (at present Y4L and Y5L are zero)

5.1.22 Carbon-nitrogen ratio (measured) of substrate
G32L= (G3L+ P018 * X02)/(Y3L + P020 * X02)

5.1.23 External breakdown (Fragmentation) ($g \cdot m^{-2} \cdot day^{-1}$)
We have assumed that this process can simply be expressed as a fraction of total carbon decomposition:
G39L= P037 * G14L
where:
P037 expresses this fraction

Each component N of the substrate will accordingly be broken down as:
G39L* YNL/G30L

5.1.24 Transport of substrate between horizons ($g \cdot m^{-2}\ day^{-1}$)
Protein-nitrogen transport from S to FH horizon on a yearly basis is given by parameter P092.

It has been assumed that this transport occurs only in the form of DO and at a constant rate during a period of approximately 200 days per year. Transport of other chemical components is calculated by knowing the C/N_1 ratio of the transported material (DO).

5.1.25 Nitrogen uptake by roots ($g \cdot m^{-2} \cdot day^{-1}$)
By making certain assumptions, the ion concentration in solution at the root surface can be deduced from the ion concentration in solution in the soil surrounding the root (Baldwin *et al.*, 1973). The concentration at the root surface is of primary interest if one assumes the rate of uptake as proportional to this concentration.

In NIING, the ion concentrations in the soil solution are calculated, and this should be the basis for the development of the ROOT module. This module will also require a certain amount of parameters which are very uncertain at present.

For that reason, N1ORG formulates nitrogen uptake by roots in a very simple way; the main interest in this model is to observe the effect of this process on other processes in the model.

We simply have:

$$G70 = P077 * \sum_{m=1}^{3} G19\ (m)$$

where:

P077 represents the fraction of mineralisation which goes to roots and G19 (m) is the mineralisation from substrate m.

By varying P077 between zero and unity we can observe the effect of uptake in decomposer growth, mineralisation etc.

5.2 Driving functions

As can be observed from the previous paragraph, in order to define G7 and G8 we need temperature and moisture at the given soil horizon. These, together with LITTER input are the three driving functions for N1ORG. They should be provided by other models, but for the time being we have simulated them with very simple analytical functions of time. These are illustrated in Fig. 2: LITTER input (formation) at FH-layer in $g \cdot litter \cdot m^{-2} \cdot day^{-1}$ (Fig. 2a), TEMPERATURE at FH-layer in º C (Fig. 2b) and MOISTURE at FH-layer in $g \cdot g^{-1}$ (Fig. 2c). The time axis in these figures covers a period of two years. Several parameters are needed in order to define these functions. Some of them can be found in Table 1: P059, P060 P065, P066, P071 and P072. Further, some parameters are needed to enable the partitioning of LITTER input into different chemical components. They can also be found in Table 1: P050 and P051.

6. Model performance

The model has been run a number of times and we have selected five of the runs for presentation and discussion here.

The first run (number 54) is the standard run, i.e. the run carried out with the values of parameters and compartments presented in tables 1 and 2 respectively. The sensitivity of the model to changes in different parameters and to changes in structure has been the object of the runs 55-58. We have investigated the sensitivity of the model (especially of mineralisation) to:

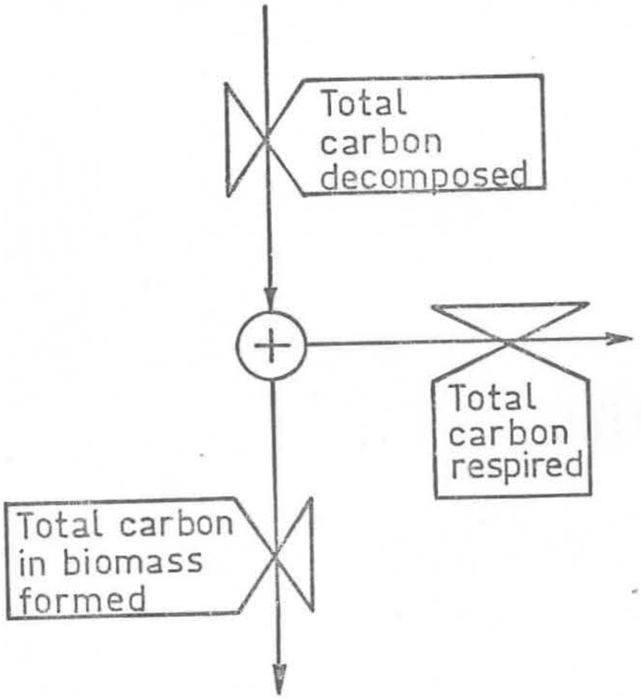
- changing the way of calculating decomposers growth (run number 55)
- changing the amount of nitrogen uptake by the roots (run number 56)
- changing the decomposers' assimilation efficiency (run number 57)
- changing the structure of the model by combining DO and HUMUS into SOM (run number 58).

At runs 54 to 57 three substrates - LITTER, DO and HUMUS - each with three compartments are present; that means P003 = P004 = 3.

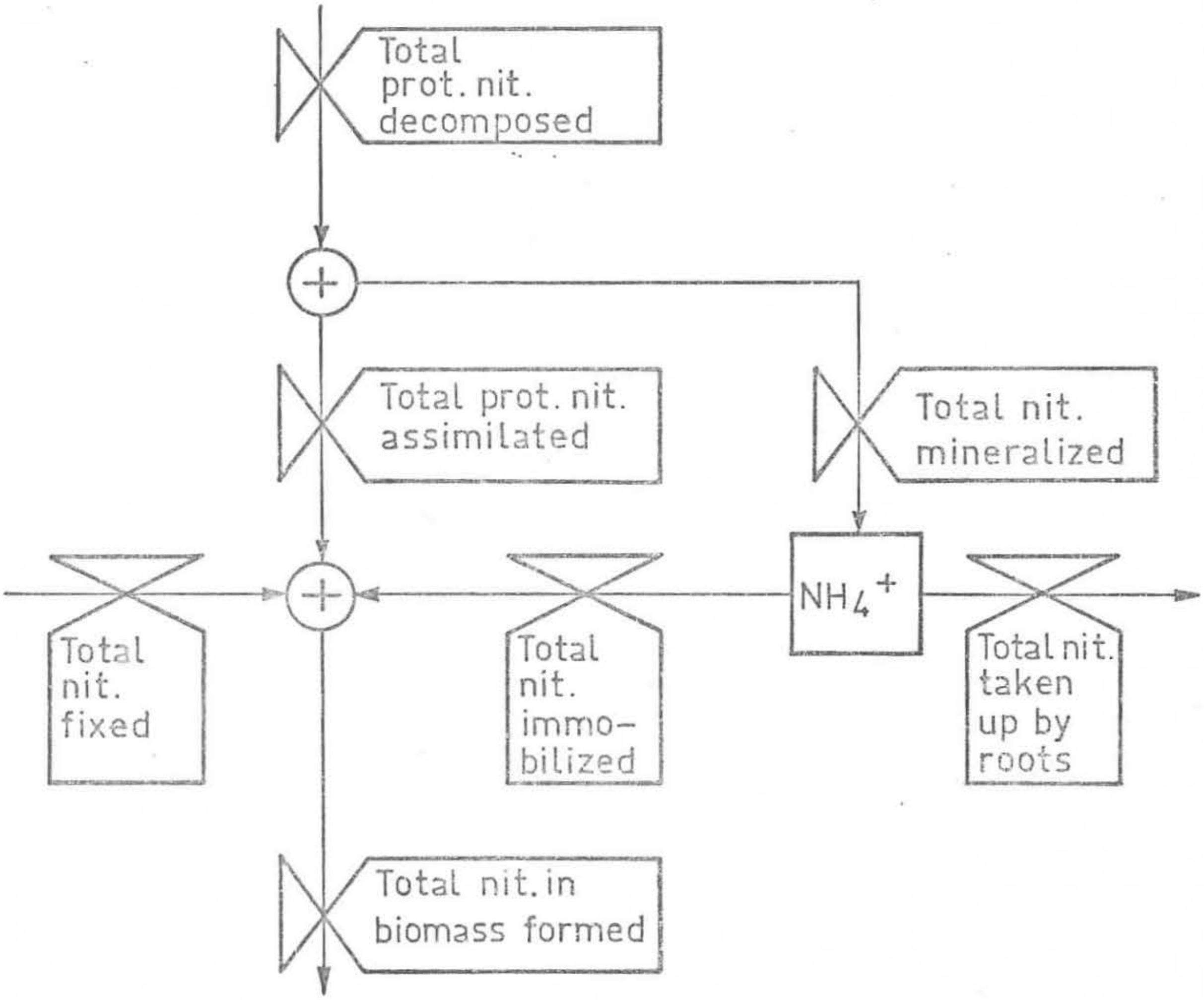
The outputs from each run of the model are shown in figures 3 to 7. The meaning of each variable symbol appearing in the figures is explained in legends to the graphs. Each run covers a period of two years, starting at July 1 ´ of a year. Euler integration has been used and the time step has been set equal to one day. The execution time has been of the order of three minutes for each run.

In order to clarify and organize the discussions around the numerical information provided by the model, two numerical flow diagrams are provided for each run. One flow diagram is for carbon, the other for nitrogen. The figures in each diagram give the accumulated amount of a given process during the two year period of the run and the unit is $g \cdot m^{-2}$ per two years.

The accumulated processes for the carbon diagram are:



For the nitrogen diagram we have:


Total prot. nit. decomposed
Total prot. nit. assimilated
Total nit. mineralized
NH_4^+
Total nit. fixed
Total nit. immo-bilized
Total nit. taken up by roots
Total nit. in biomass formed

6.1 Standard run - run number 54

In this run we have taken:

- P017 = 1., i.e., biomass formation is calculated with the function for mean growth (5.1.10) and
- P077 = 0., i.e., nitrogen uptake by roots has been set equal to zero.

We can see from fig. 3-a that the model appears relatively stable, at any rate during the two year run. The steady increase in the compartment for inorganic nitrogen (X01) is caused by the absence of uptake by roots; G70 being zero all the time, Fig. 3-b.

The behaviour of compartment (X02) is not in total agreement with known facts from the Jädraås site. Fungal biomass, which predominates, is low in the dry period in July and August and increases in the autumn and in April-May, that is, the biomass is high during the wet periods (Söderström, pers. comm.).

It is difficult to comment on the compartments for litter as we do not yet have information about the root litter dynamics. The compartments for dead organisms and humus show little variation and it is difficult to verify the variation obtained.

The remaining G-functions have a typical form (Fig. 3-b) caused by the temperature and moisture modulation of biomass growth.

In Fig. 3-c we can observe several facts which are direct consequences of the hypoteheses in the model.

With the values given to parameters P018, P019 and P020 (Table 1), the resulting critical C/N ratio is equal to 100. The initial C/N_1 values for LITTER, DO and HUMUS are 90, 10 and 3204 respectively. This means that only LITTER and DO will mineralise nitrogen; which is confirmed by the plots of G19L, G19DO and G19H. One of the conclusions presented by Parnas (1975a)* is that a material with a lower carbon-nitrogen ratio than the critical value will not change its carbon-nitrogen ratio as decomposition goes on. This is confirmed by the plots of G4L and G4DO. On the other hand, a material with a higher carbon-nitrogen ratio than the critical value will have an increase in its carbon-nitrogen ratio if none or little NH_4^+ is present in the system. This is confirmed by the plot of G4H (HUMUS carbon-nitrogen ratio): it increased from 3204 (initial) to 3208 (final). This has been so, even considering the break-down of LITTER and D.O. which should tend to decrease the HUMUS carbon-nitrogen ratio.

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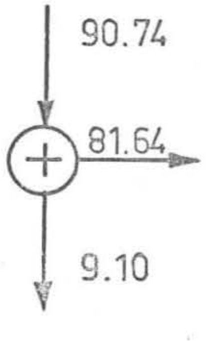
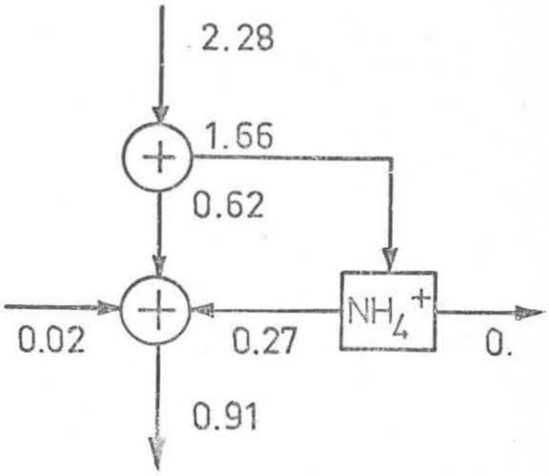
* Most of the conclusions presented here are of a general nature, regardless of the actual way used to calculate decomposers growth. They are a consequence of the hypothesis on which the model is based. So, such conclusions are valid here, even if we at this run have used mean growth instead of stationary growth to calculate biomass formation.

The "measured" C/N ratio (substrate plus biomass) behaves in a more complicated way: G32L, G32DO, G32H The variation of the C/N ratio in litter (G32L) appears reasonable.

The decomposer time of growth (5.1.10.) was more than two months for the three substrates LITTER, D.O. and SOM-carbons (G22L, G22DO G22H).

The carbon and nitrogen diagrams for this run are as follows:





The contributions from LITTER, D.O. and HUMUS to the total decomposed carbon (90.74) were 76.22, 14.34 and 0.18 respectively. Respiration and mineralisation mean values for the period of the run are 0.1134 and 0.0023 g · m^{-2} day^{-1} respectively. The respiration value (83 g for 2 years) might be low compared with the value of 120-200 g C suggested by Staaf (pers. comm.). Unfortunately it is not possible to evaluate the mineralisation rate.

Conclusion 4 by Parnas (1975 a) states: "The rate of mineralisation is increased as C/N_1 is decreased". This is confirmed here: To the 1.66 g m^{-2} of nitrogen mineralised during the two years the contribution from LITTER and D.O. were 0.33 and 1.33 g m^{-2} respectively.

6.2 "Stationary growth" for decomposers - run number 55

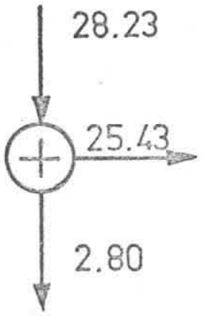
In this run we have

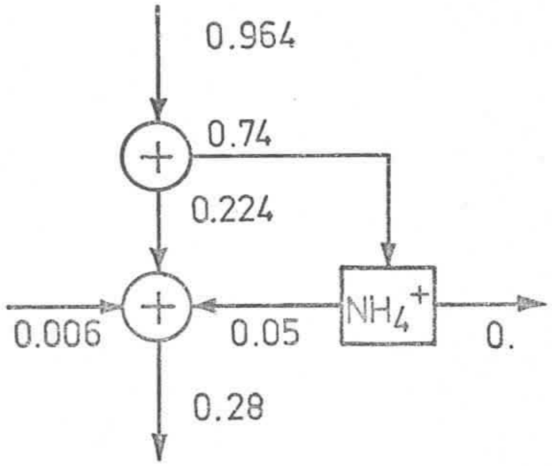
- P017 = 0. i.e. biomass formation is calculated with stationary growth (5.1.10.), and
- P077 = 0. as before

Fig. 4-a shows that the model behaviour is not as good as in the previous run: LITTER and D.O. compartments increase with time, while BIOMASS compartment (X02) decreases.

With the exception of that, most of what has been said about general trends for the previous run also holds for this one.

The carbon and nitrogen diagrams are now:





The contributions of each material to carbon are: 20.54 for litter, 7.38 for D.O. and 0.31 for humus. Regarding nitrogen mineralisation the contributions are: 0.68 for D.O. and 0.06 for litter. The respiration and mineralisation mean values are 0.040 and 0.001 g m^{-2} day^{-1} respectively.

The lower figures from this run are a consequence of the behaviour of the compartments. One possible way to improve this could be to change the Michaelis-Menten parameters (see Table 1), the mortality parameter or the optimal growth parameters. Besides the complications involved, it is known that the use of this kind of formulation to simulate decomposer growth in natural systems has been criticised. Thus, at this point, a sound decision seems to go on with the formulation of growth used in run 54. In the runs to follow it will be understood that the mean growth is used to calculate biomass formation.

6.3 Effect of nutrient uptake by roots - run number 56

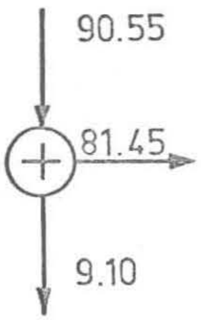
Now, we have:

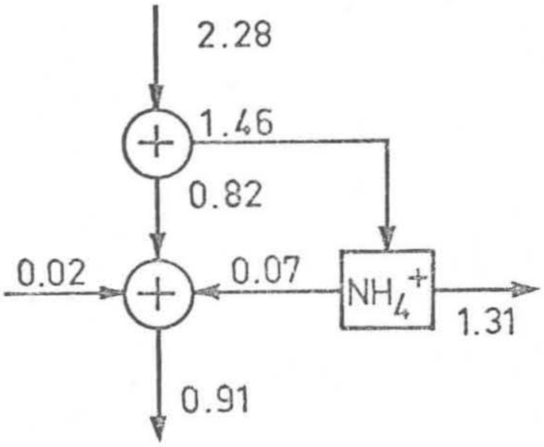
- P077 = 0.9 (uptake by roots is included)

The effects of this change in the root parameter can be seen in Fig. 5-a; the NH_4^+ values (X01) are now one order of magnitude lower than in run 54. The nitrogen uptake rate is shown by G70 in Fig. 5-b.

The general trends discussed in run 54 are, of course, not modified by the new process and decreased NH_4^+-level.

Some new, interesting facts can be noticed, however. Before these are discussed, we present the flow diagrams:





As before, the contributions to decomposed carbon are: 76.08 for litter, 14.30 for D.O. and 0.17 for humus. The contributions to mineralisation amount to 0.16 for litter and 1.30 for D.O. Respiration and mineralisation mean values are 0.1132 and 0.0020 g m^{-2} day^{-1} and thus, respiration might also be low here with 83 g versus 120-200 as estimated by Staaf (pers. comm.).

One major change that has taken place in the nitrogen flow, is that immobilisation is considerably lower than it was in run 54: 0.07 against 0.27. This is not surprising considering that NH_4^+ has been removed from the system. Since the rate of immobilisation is set to be proportional to the instantaneous fraction of NH_4^+ in the system (5.1.19) the result is not surprising. Less expected is the decrease in mineralisation rate: 1.46 against 1.66 at run 54. This is, however, in agreement with one of the conclusions given by Parnas (1975 a). This is: "Conclusion 5. The higher the amount of NH_4^+ in the area, the higher will be the rate of mineralisation". In other words: the higher the amount of nitrogen taken up by the root system, the lower will be the rate of nitrogen mineralisation.

It is important to notice that the biomass dynamics has practically not been influenced by the new process: the mean value of X02 has been 16.95 for run 54 and 16.94 for the present run. The biomass formed has been 18.15 at run 54 and 18.11 at the present run.

This has two important consequences:

- first, the amount of nitrogen required for growth is the same at both runs: 0.91. As immobilisation is now lower, the decomposers must have recourse to organic nitrogen: 0.82 against 0.62 at run 54,
- second, the decomposed amount of organic nitrogen is the same for both runs: 2.28. As a consequence of all this; the organic nitrogen surplus turns out to be lower at this run.

6.4 Effect of changing decomposer assimilation efficiency - run number 57

One important parameter in the model is the biomass efficiency in carbon utilisation: P019. It derives its importance from, among other things, the fact that it is one of the parameters determining the critical C/N ratio (5.1.6).

The higher this parameter value, the lower will be the critical C/N ratio in the model. This could indicate that the model should be very sensitive to changes in this parameter.

In order to test this, P019 was doubled in this run and thus the critical carbon-nitrogen ratio went down to 50.Thus,in this run:

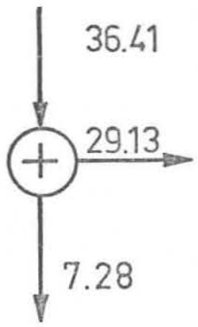
- P019 = 0.2

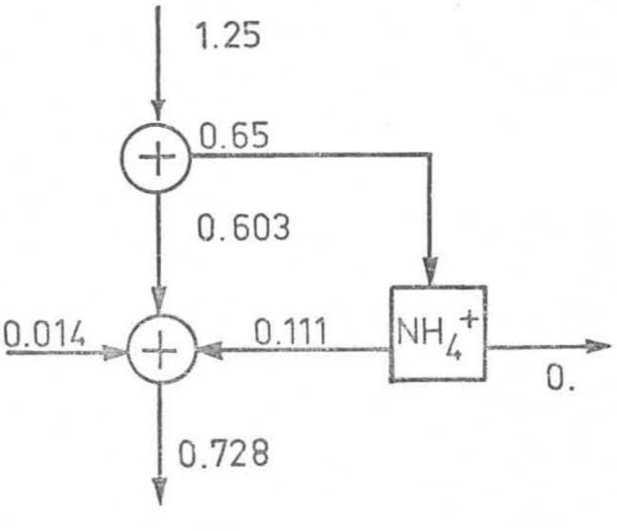
Fig. 6-c shows some expected results:

- G19L equals zero; i.e. there is no mineralisation from litter. This lack of mineralisation from litter might differ from reality (Popovič, 1976)
- G4L (C/N_1 in litter) increases from 90 (initial) to 96

Fig. 6-a shows that the litter compartment tends to increase at this run.

The flow diagrams are now:





The contributions to total carbon decomposed are: 28.46 from litter, 7.88 from D.O. and 0.07 from humus. Clearly, in this case all mineralisation came from D.O. The mean values for respiration and mineralisation are 0.040 and 0.001 g m^{-2} day^{-1} respectively. The respiration value (30 g for 2 years) apparently is low compared with that given by Staaf (pers. comm.) on 120-200.

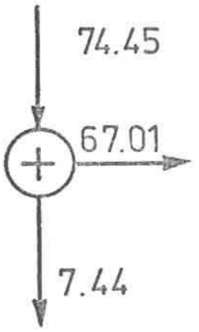
6.5 Effect of simplifying model structure; HUMUS and D.O. combined in SOM - run number 58

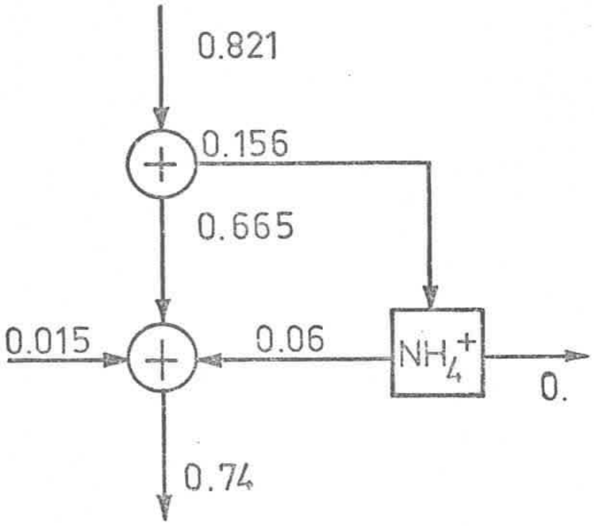
As stated previously, in this run D.O. and humus are clustered together in SOM.

Fig. 7-a shows that the litter compartment behaved, approximately in the same way as in run 54. The SOM compartment increased with time; this is due to the fact that the value for optimal growth on humus has now been used for SOM (a mean value between those of D.O. and humus should, instead, have been used).

The fact that mortality now actually gave an input to SOM by the model can be verified by looking at graph G4S in Fig. 7-c. It is due to this input that the carbon-nitrogen ratio in SOM decreases from 466 (initial) to 356 (final).

Mineralisation from SOM - G19S - is equal to zero, as it should be. The flow diagrams for this run are:





To the total carbon decomposed, LITTER has contributed with 73.11 g m^{-2} and SOM with 1.34 g m^{-2}. All mineralised nitrogen now came from litter. This apparently is not true for the FH-layer (Popovič, 1976). The respiration and mineralisation yearly mean values were: 0.0930 and 0.0002 g m^{-2} day^{-1} respectively - the respiration might be low.

7. Conclusions

The runs discussed in the previous section show that:

- the model behaves, at present, in the way that should be expected from theoretical (analytical) considerations
- the model is a convenient tool to analyse the effects produced on some processes when changes in parameters and in structure are introduced
- the model predicts values for decomposers respiration and nitrogen mineralisation which seem to be lower than estimated values obtained from measurements.

At this point, what seems to be needed most are experimental data to further modify, build, and verify the model. For planning this further work a convenient next step would be to carry out a more extensive sensitivity analysis with the present model.

8. References

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Comments on some parameters used (Table 1)

There are too few measurements on processes and compartments from the Ih VA site to allow of too deep an analysis of the values obtained in the runs. A short discussion of some parameter values might be fruitful.

One important parameter is the assimilation efficiency (P019). This parameter is unfortunately very uncertain. The fractions of carbon and nitrogen in decomposer biomass (P018 and P020) are difficult to determine and it is possible that the literature values obtained might have to do. The optimum growth values in litter, humus and on dead organisms (P027-P029) are not determined - the values are chosen by making a rough estimate. The mortality rates (P032 and P033) are taken from Parnas and Redford (1974). The work by Söderström on estimating the death rate for fungi might give or confirm the size of this process.

P037 is estimated from some preliminary decomposition values and P038 is just a rough estimate.

P050-P051 in root litter are not determined and needle litter values are used here.

The relative response of microorganisms to moisture and temperature (P005-P012) are so far represented by two simple functions. This response has a central role in the model.

The dynamics of the root litter input is shown in Fig. 2 a. The input values (P059, P060) are given as a first approximate value by Persson (pers. comm. and the input dynamics are so far approximated due to lack of information. This parameter will be improved shortly.

The fraction of the microorganisms that can fix nitrogen (P021) is set at 2%, a figure that will probably do.

The transport of solid nitrogen from the S- to the FH-layer (P092) is discussed in section 5.1.24. The calculation is made from incomplete data but the value will hopefully be improved shortly.

Table 1. The most important parameters in N1ORG

Symbol	Meaning	Typical value	References
P001	No. of litter fractions	1	
P002	Code parameter to define structure		
P003	No. of litter or humus boxes	3	
P004	No. of D.O. boxes	3	
P005	Temperature scale factor (5.1.7)	-2.°C	
P006	-"-	20.°C	
P007	-"-	27.°C	
P008	-"-	37.°C	
P009	Moisture scale factor (5.1.8)	0.28 $g \cdot g^{-1}$	
P010	-"-	0.65 $g \cdot g^{-1}$	
P011	-"-	1.60 $g \cdot g^{-1}$	
P012	-"-	4.50 $g \cdot g^{-1}$	
P017	Switch (see 5.1.10)	0 or 1	
P018	Fraction carbon in biomass (5.1.5)	0.5	Söderström, pers. comm.
P019	Assimilation efficiency (5.1.5)	0.1	"-
P020	Fraction nitrogen in biomass (5.1.6)	0.05	"-
P021	Fraction biomass which fixes nitrogen (5.1.13)	0.02	Granhall, pers. comm.
P027	Optimal growth in litter(5.1.9)	0.005 day^{-1}	
P028	"- D.O.	0.0015 day^{-1}	
P029	"- humus	0.0001 day^{-1}	
P032	Normal mortality rate (5.1.11)	0.0015 day^{-1}	Parnas & Redford (1974)
P033	Starvation rate (5.1.11)	0.02 day^{-1}	"-
P034	Protein C/N ratio (5.1.14)	4	Parnas (1975a)
P037	Litter breakdown (5.1.23)	0.1	
P038	D.O. "- "-	0.1	
P050	Fraction protein carbon in litter input at FH level	0.02	
P051	Fraction other carbon in litter input at FH level	0.43	
P059	Daily litter input during spring (FH level)	1.5 $g\ m^{-2} day^{-1}$	Persson, pers. comm.

Symbol	Meaning	Typical value	References
P060	Daily litter input during autumn (FH level)	1.5 g $m^{-2}day^{-1}$	Persson, pers. comm.
P065	Maximum temperature of year	15.^{o}C	Measured value (Problem area 2)
P066	Minimum temperature of year	-3.^{o}C	"-
P071	Maximum moisture of year	4. $g \cdot g^{-1}$	"-
P072	Minimum moisture of year	0.5 $g \cdot g^{-1}$	"-
P077	Mineralisation fraction which goes to roots (5.1.25)	0 to 1	
P080	Litter carbon Michaelis-Menten parameter (5.1.10)	20.0 $g \cdot m^{-2}$	Parnas (1975a)
P081	D.O. "-	1.0 $g \cdot m^{-2}$	"-
P082	Humus "-	20. $g \cdot m^{-2}$	"-
P085	Litter nitrogen Michaelis-Menten parameter (5.1.10)	1.0 $g \cdot m^{-2}$	"-
P086	D.O. "-	1.0 $g \cdot m^{-2}$	"-
P087	Humus "-	1.0 $g \cdot m^{-2}$	"-
P092	Protein-nitrogen transport from S to FH horizon (5.1.24)	0.145 g $m^{-2}yr^{-1}$	present paper

Comments on the initial compartment values (Table 2)

It appears that in the FH-layer we have measured initial values for the compartments fairly well - an exception is of course the compartment for dead organisms in which case the correct order of magnitude would be as close as we could hope to come. The dynamics of the compartments is less well known.

Inorganic nitrogen in the FH-layer has been measured by Popovič (1975, 1976) and varies between 27 and 53 mg/m^2 in the period from May and to November.

The litter compartments (Y1L,Y2L,Y3L) have been measured (Persson, pers. comm.) and the values obtained appear to do for the model. The dynamics of the root litter compartment which will be determined will be very useful to verify the variation obtained by the model. There is a lack of analysis on root litter, however, and the values for protein-carbon and-nitrogen as well as other carbon were taken from analysis carried out on needle litter. It is possible that they are not correct.

The biomass compartment is dominated by fungal and bacterial biomass (Bringmark *et al.* 1975) and only the values for these are used. The variations during the year might be large- it is known that the biomass decreases in the dry period from June to August and is high in spring and in autumn (Söderström, pers. comm.). Owing to lack of information the size of the compartment has, as an approximation, been given the initial value of double the fungal biomass.

The humus compartment has been measured (Staaf & Berg, in manuscript) and it appears that the value obtained is good enough.

The compartment for dead organisms has been roughly estimated as a fraction of the biomass compartment.

Table 2 NIORG compartments (initial values)

The compartments and their initial values for a typical run. The structure for this run is: one soil horizon (FH), three organic materials, and three boxes for each material.

Symbol	Meaning	Value	Reference
X01	NH_4^+	0.1 g.m^{-2}	Popovic (1975, 1976)
X02	Decomposer biomass	15.0 "-	Söderström, pers. comm.
Y1L	Litter protein-carbon	7.0 "-	present paper
Y2L	Litter other carbon	150.5 "-	"-
Y3L	Litter protein-nitrogen	1.75 "-	"-
Y1DO	D.O. protein-carbon	12.0 "-	Söderström, pers. comm.
Y2DO	D.O. other carbon	18.0 "-	"-
Y3DO	D.O. protein-nitrogen	3.0 "-	"-
Y1H	Humus protein-carbon	2.0 "-	present paper
Y2H	Humus other carbon	1600.0 "-	"-
Y3H	Humus protein nitrogen	0.5 "-	"-

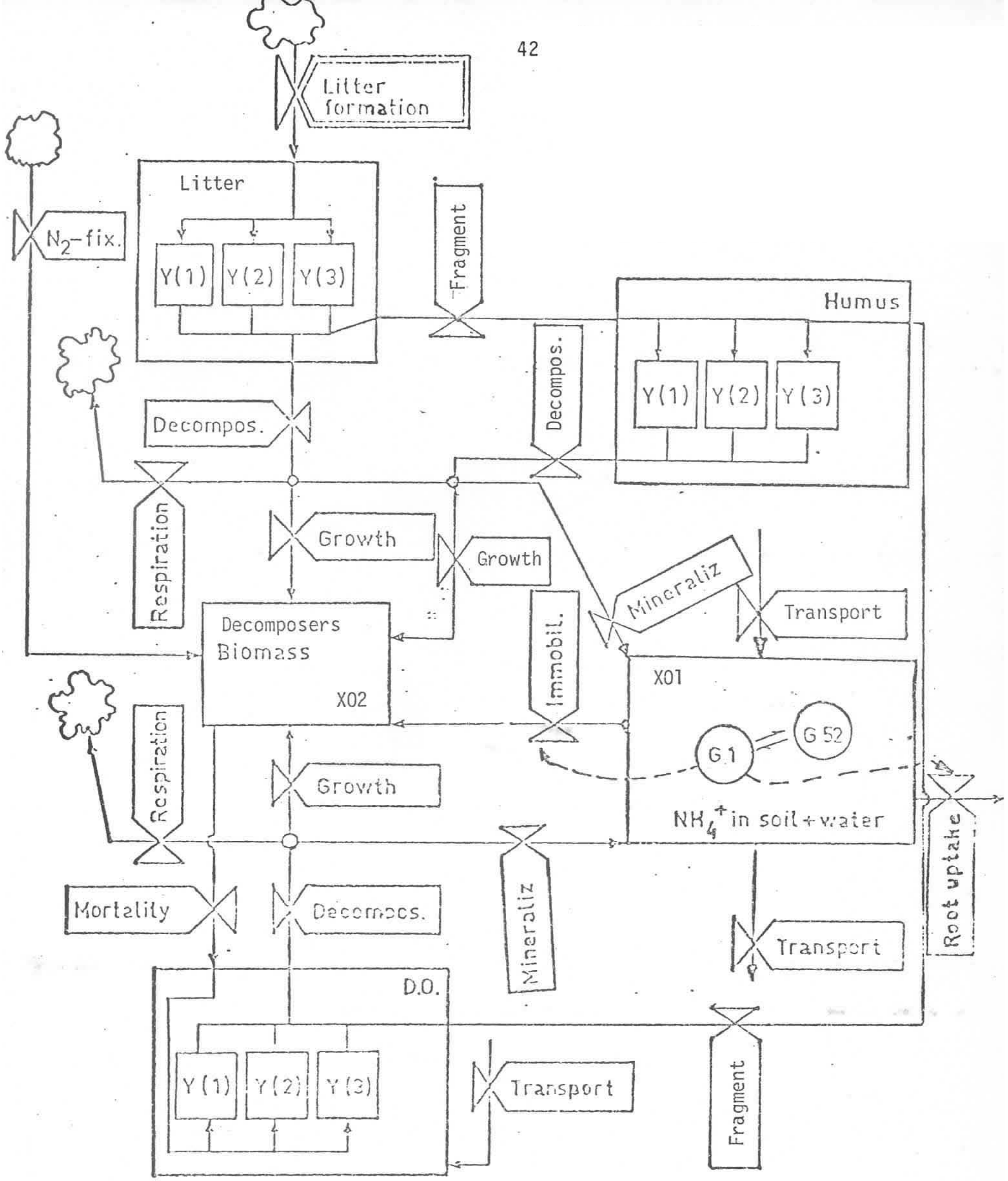


Fig. 1-a NIORG in FH – layer with HUMUS and DO separate

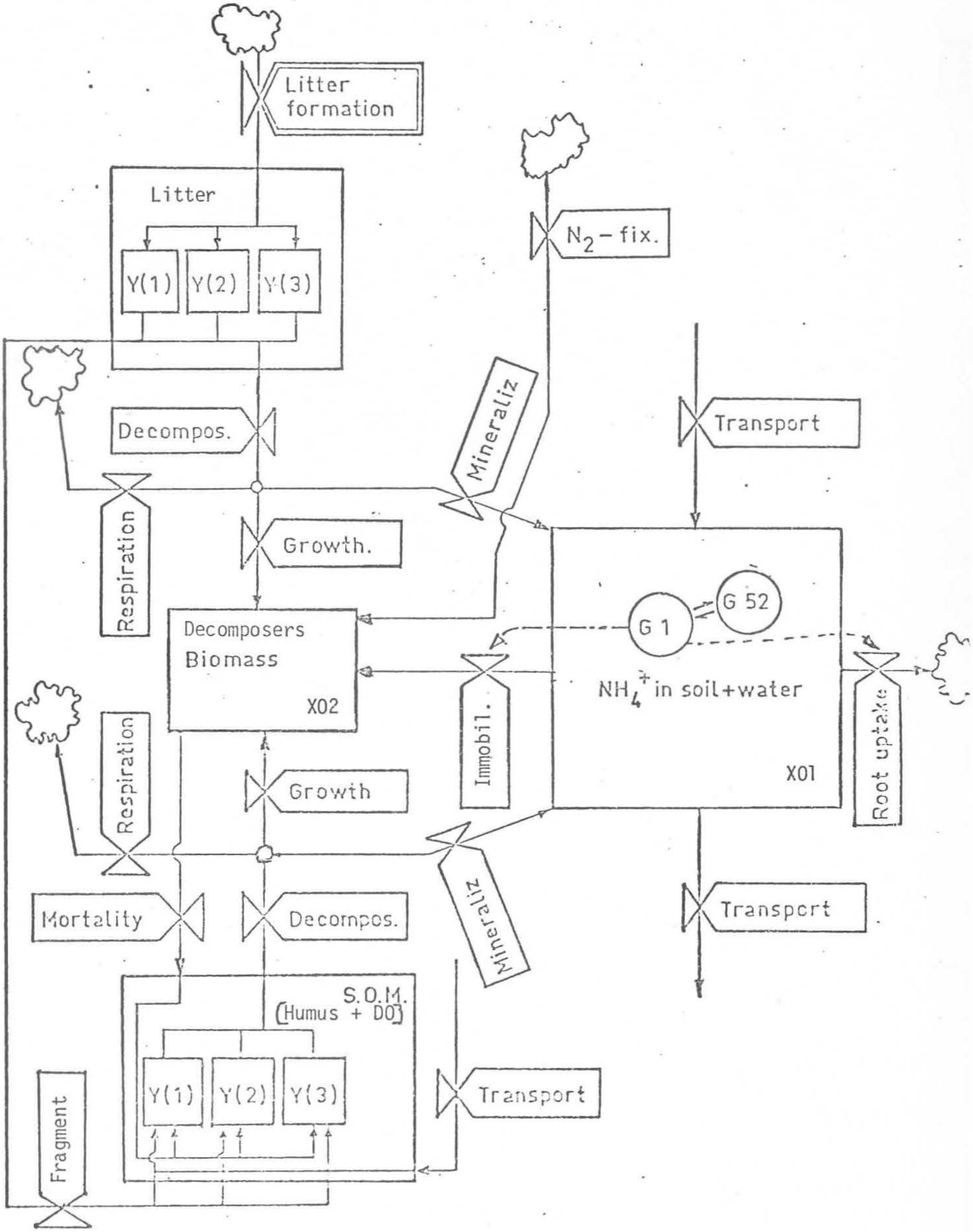
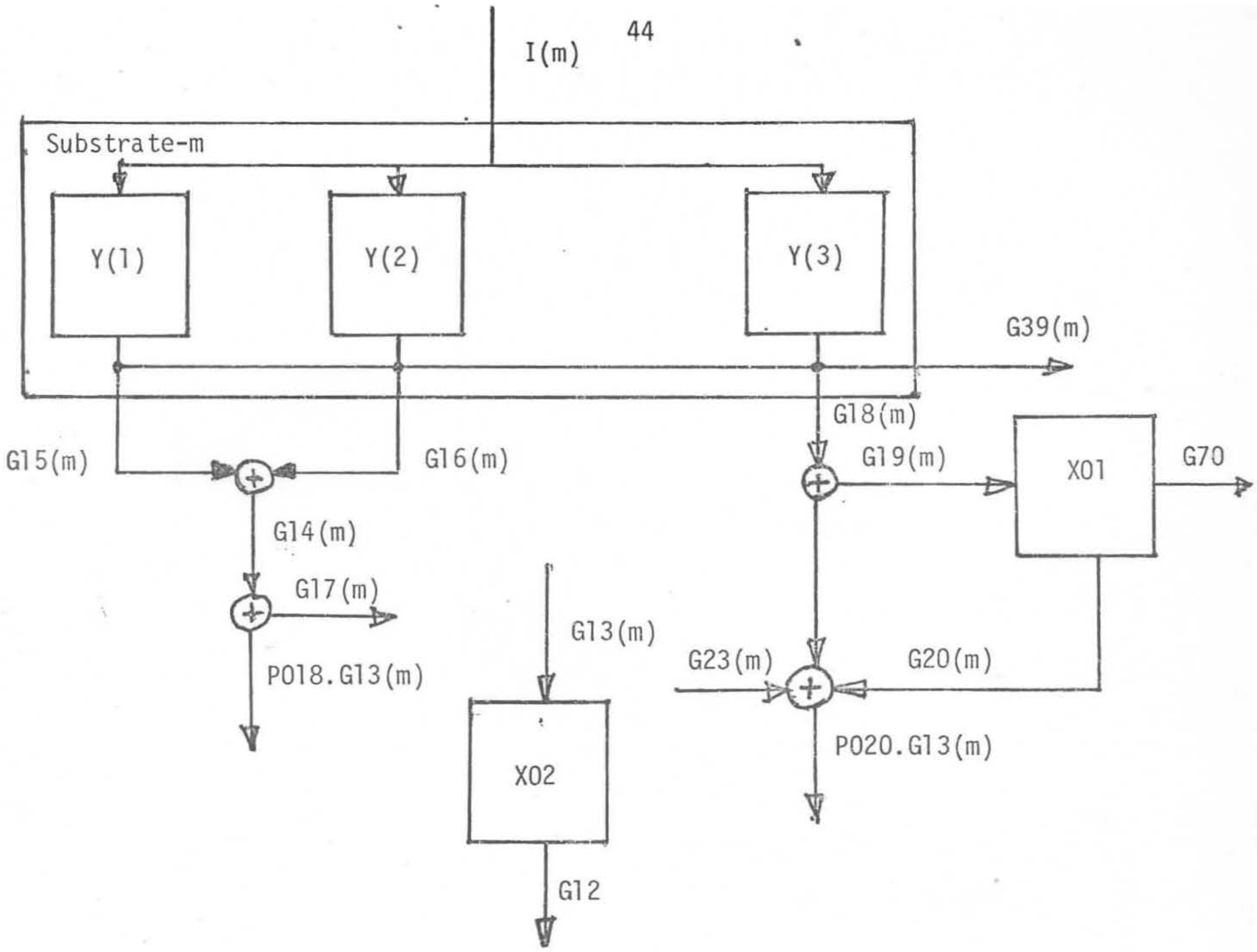


Fig. 1-b NIORG in FH-layer with HUMUS and DO combined



I(m) Input to substrate-m

G39(m) Substrate-m fragmentation (external break-down)

CARBON

Y(1)	substrate-m protein-carbon
Y(2)	substrate-m other carbon
G15(m)	substrate-m protein-carbon decomposition
G16(m)	substrate-m other carbon decomposition
G14(m)	substrate-m carbon decomposition
G17(m)	decomposers respiration from substrate-m
P018.G13(m)	decomposers carbon demand from substrate-m

DECOMPOSERS

X02	decomposers biomass in the soil layer
G13(m)	biomass formation from substrate-m (growth)
G12	decomposers mortality

NITROGEN

Y(3)	substrate-m protein-nitrogen
X01	inorganic nitrogen in the soil layer
G18(m)	substrate-m protein-nitrogen decomposition
G19(m)	substrate-m mineralisation
G20(m)	immobilization corresponding to substrate-m
G23(m)	nitrogen fixation corresponding to substrate-m
G70	nitrogen uptake by roots in the soil layer
P020.G13(m)	decomposers nitrogen demand from substrate-m

Fig. 1-c A schematical representation of the decomposition of a substrate (m) in a soil layer.

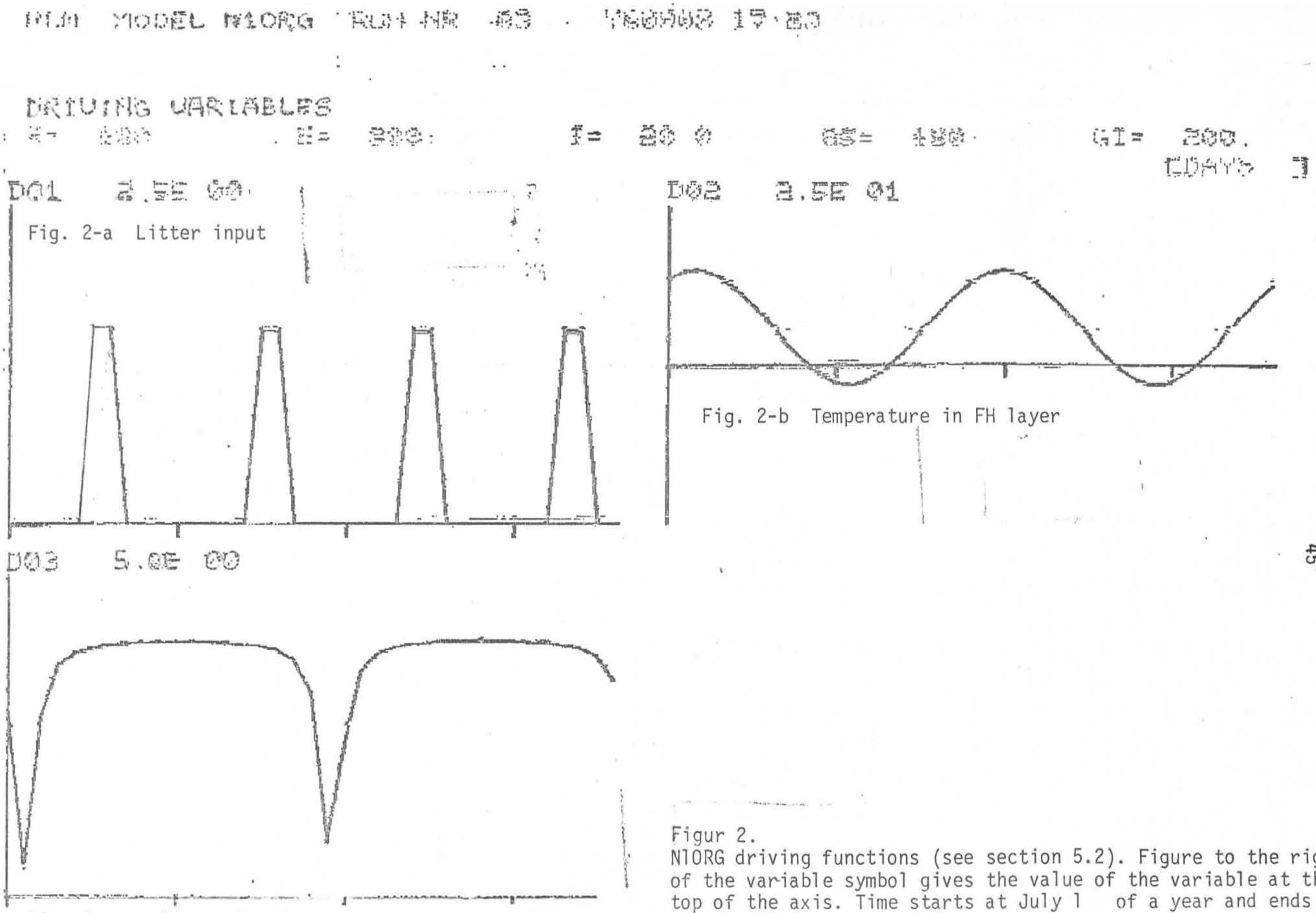


Fig. 2-a Litter input

Fig. 2-b Temperature in FH layer

Fig. 2-c Moisture in FH layer

Figur 2.
N1ORG driving functions (see section 5.2). Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each **step** of the time axis represents 200 days.

Figs. 3-7 Legends to N1ORG graphs

Symbol	Meaning	Units
G13T	Total biomass growth	g biomass m^{-2} day^{-1}
G17T	Total respiration	g carbon m^{-2} day^{-1}
G19T	Total nitrogen mineralisation	g nitrogen m^{-2} day^{-1}
G20T	Total nitrogen immobilisation	"-
G21T	Net nitrogen mineralisation	"-
G23T	Total nitrogen fixation	"-
G70	Nitrogen uptake by roots	"-
G13L	Biomass growth from litter	g biomass m^{-2} day^{-1}
G22L	Growth time in litter	months
G14L	Litter carbon decomposition	g carbon m^{-2} day^{-1}
G30L	Total amount of litter	$g \cdot m^{-2}$
G4L	Litter C/N_1 ratio	-
G32L	Litter C/N ratio (measured)	-
G19L	Nitrogen mineralization from litter	g nitrogen m^{-2} day^{-1}
G13DO	Biomass growth from D.O.	g biomass m^{-2} day^{-1}
G22DO	Growth time in D.O.	months
G14DO	D.O. carbon decomposition	g carbon m^{-2} day^{-1}
G30DO	Total amount of D.O.	$g \cdot m^{-2}$
G4DO	D.O. C/N_1 ratio	-
G32DO	D.O. C/N ratio (measured)	-
G19DO	Nitrogen mineralisation from D.O.	g nitrogen m^{-2} day^{-1}
G13H	Biomass growth from humus	g biomass m^{-2} day^{-1}
G22H	Growth time in humus	months
G14H	Humus carbon decomposition	g carbon m^{-2} day^{-1}
G30H	Total amount of humus	$g \cdot m^{-2}$
G4H	Humus C/N_1 ratio	-
G32H	Humus C/N ratio (measured)	-
G19H	Nitrogen mineralization from humus	g nitrogen m^{-2} day^{-1}
X01-Y3H	Compartments as defined in table 2	

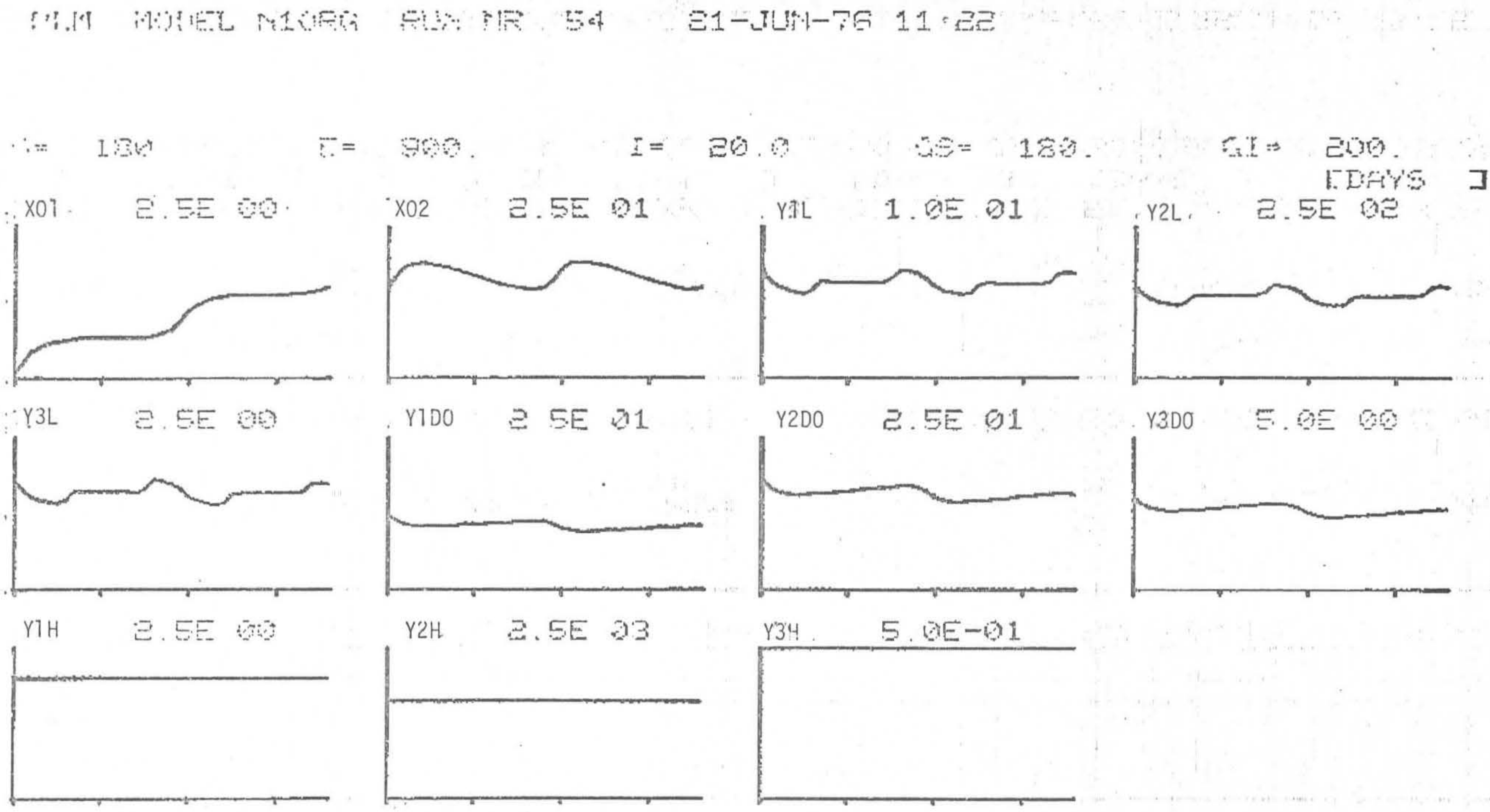


Fig. 3-a Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each **step** on the time axis represents 200 days.

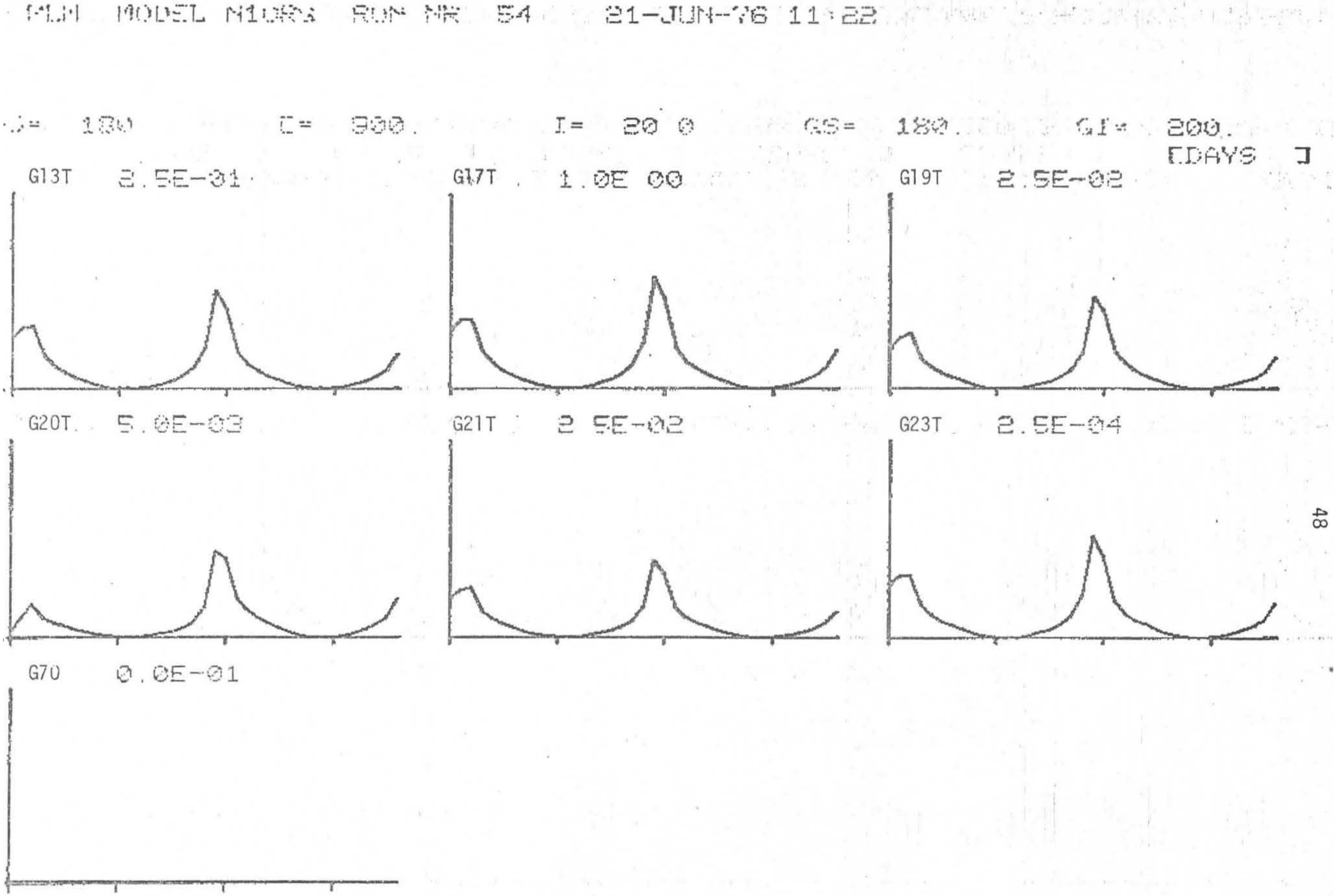


Fig. 3-b Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

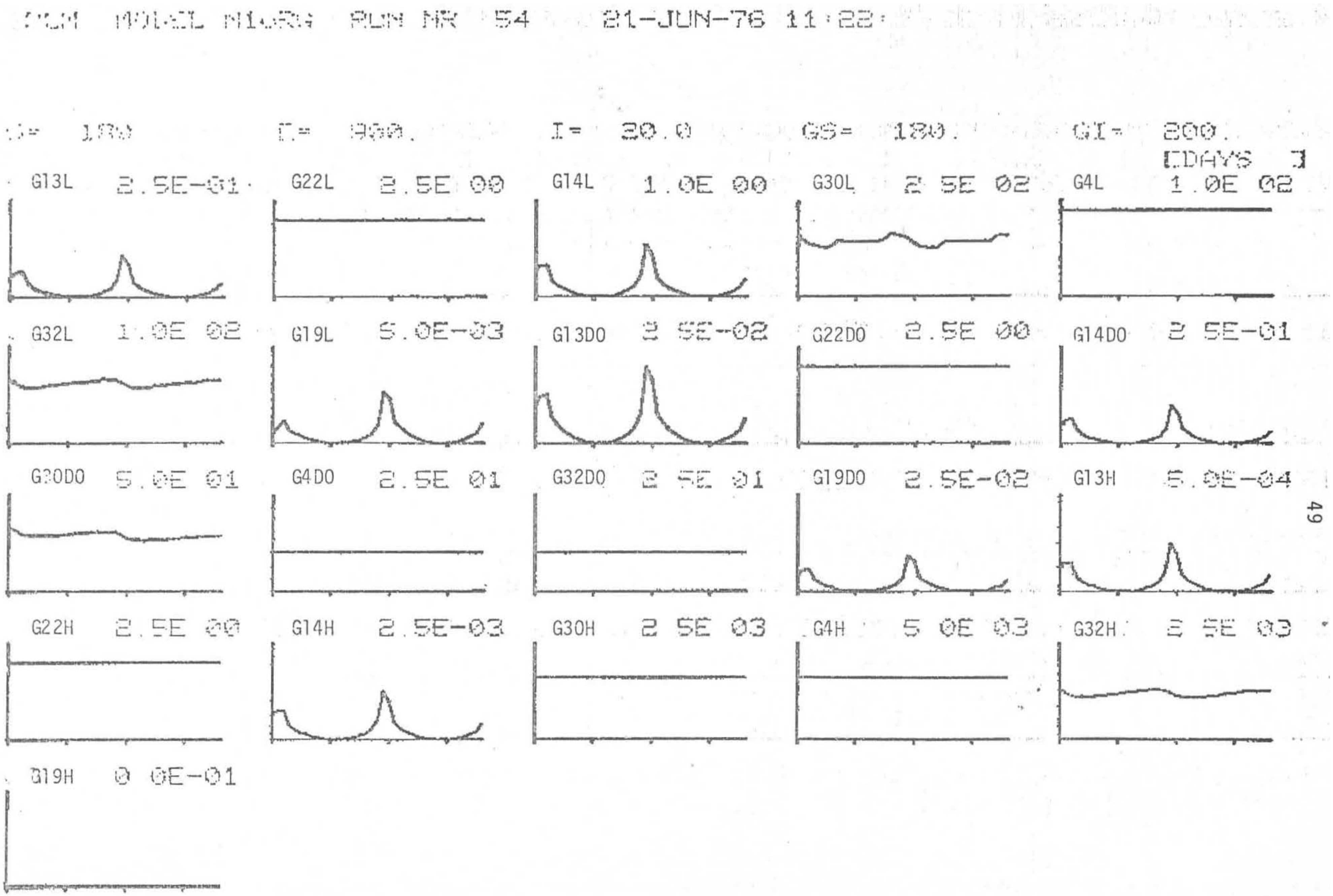


Fig. 3-c Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

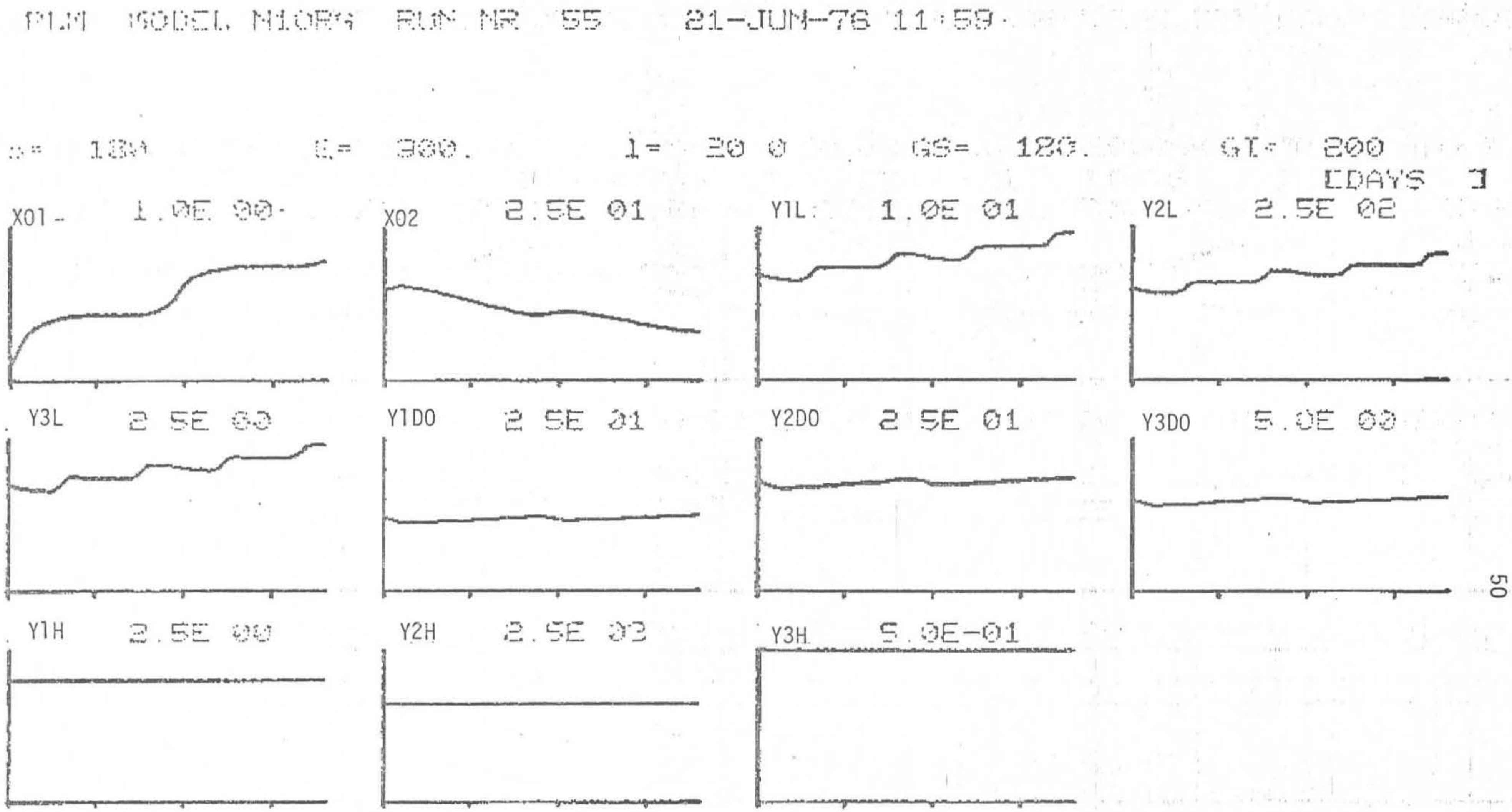


Fig. 4-a Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

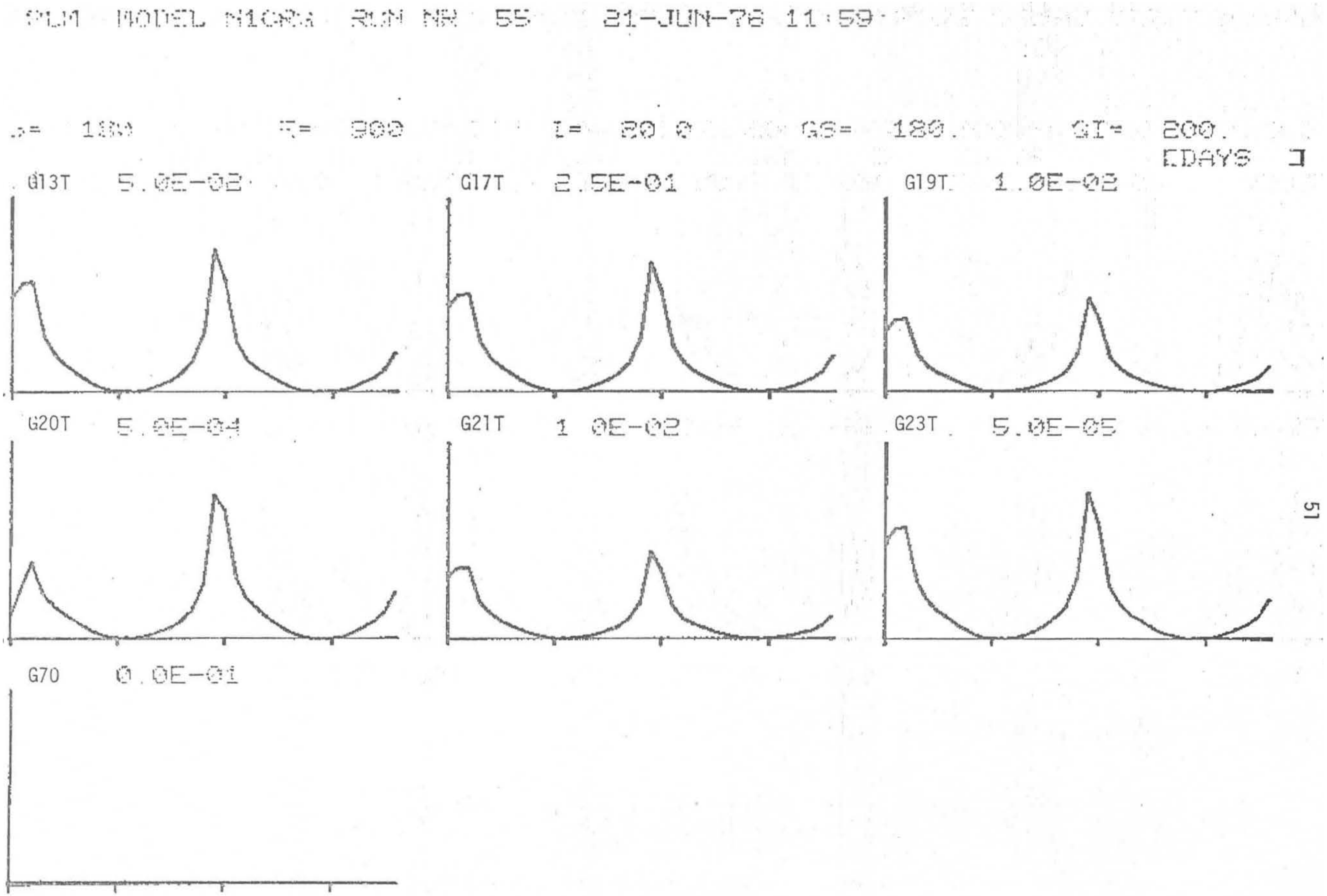


Fig. 4-b Variables defined in legends:Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

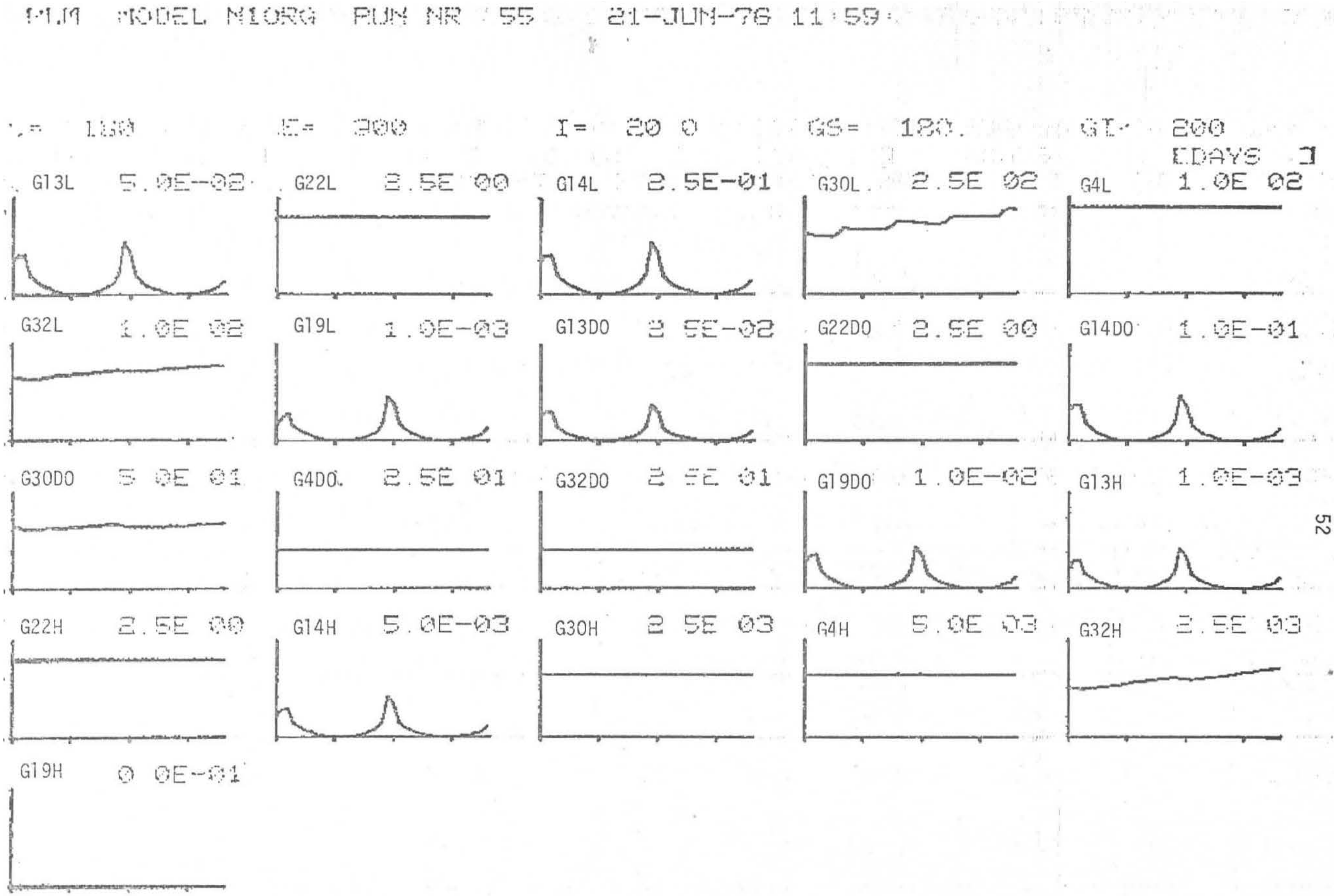


Fig. 4-c Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

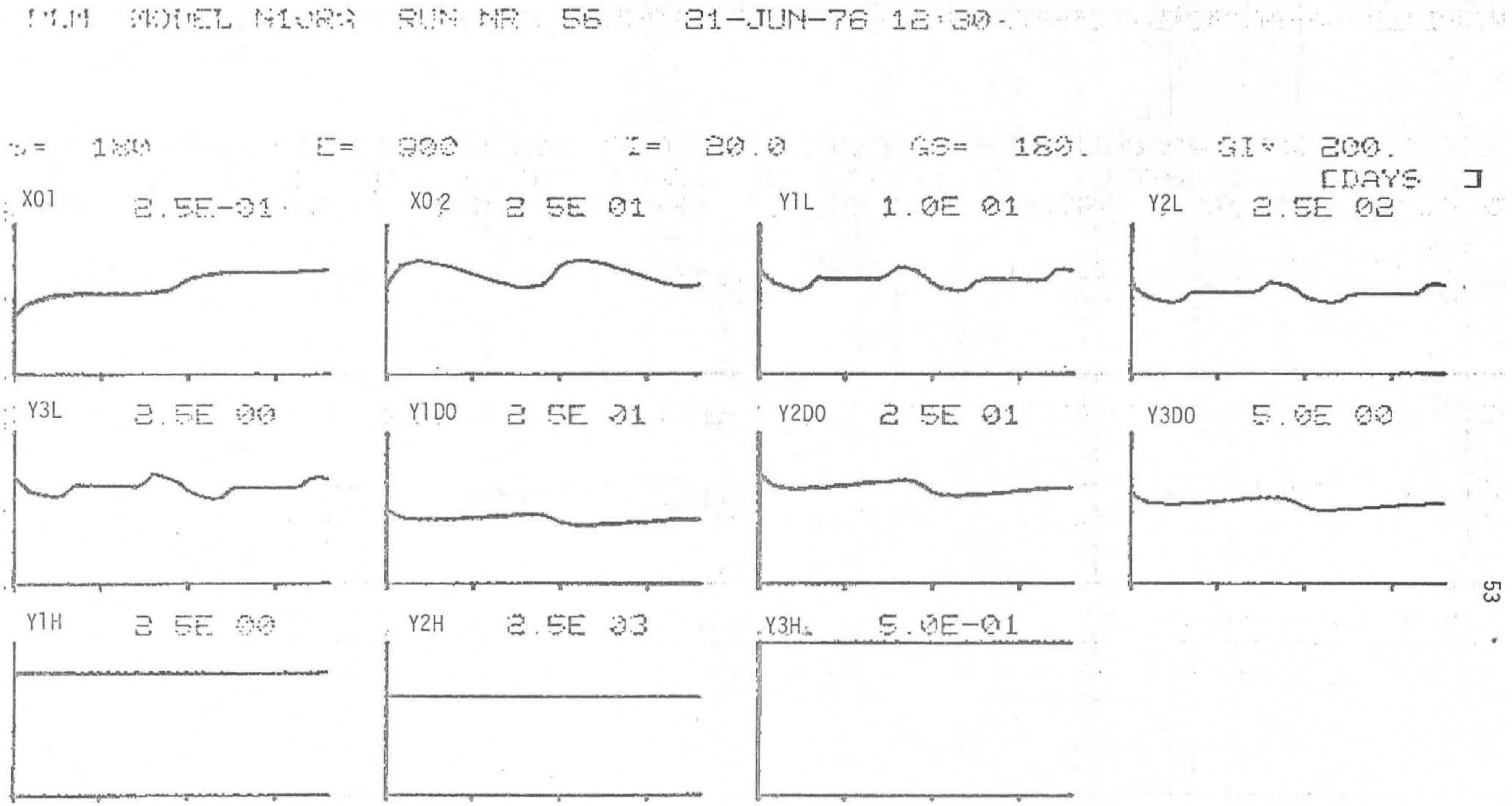


Fig. 5-a Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1st of a year and ends two years later; each step on the time axis represents 200 days.

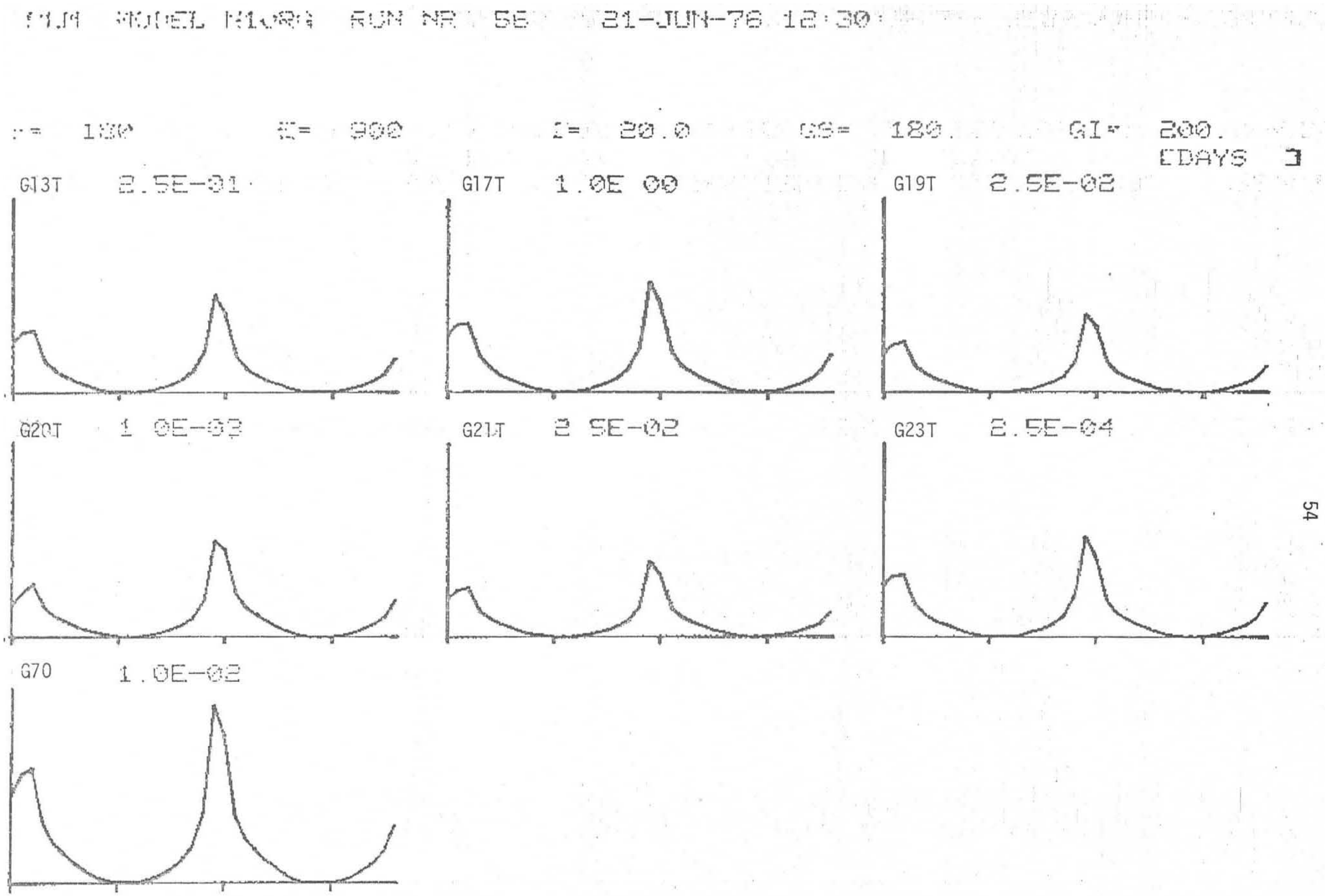


Fig. 5-b Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1st of a year and ends two years later; each step on the time axis represents 200 days.

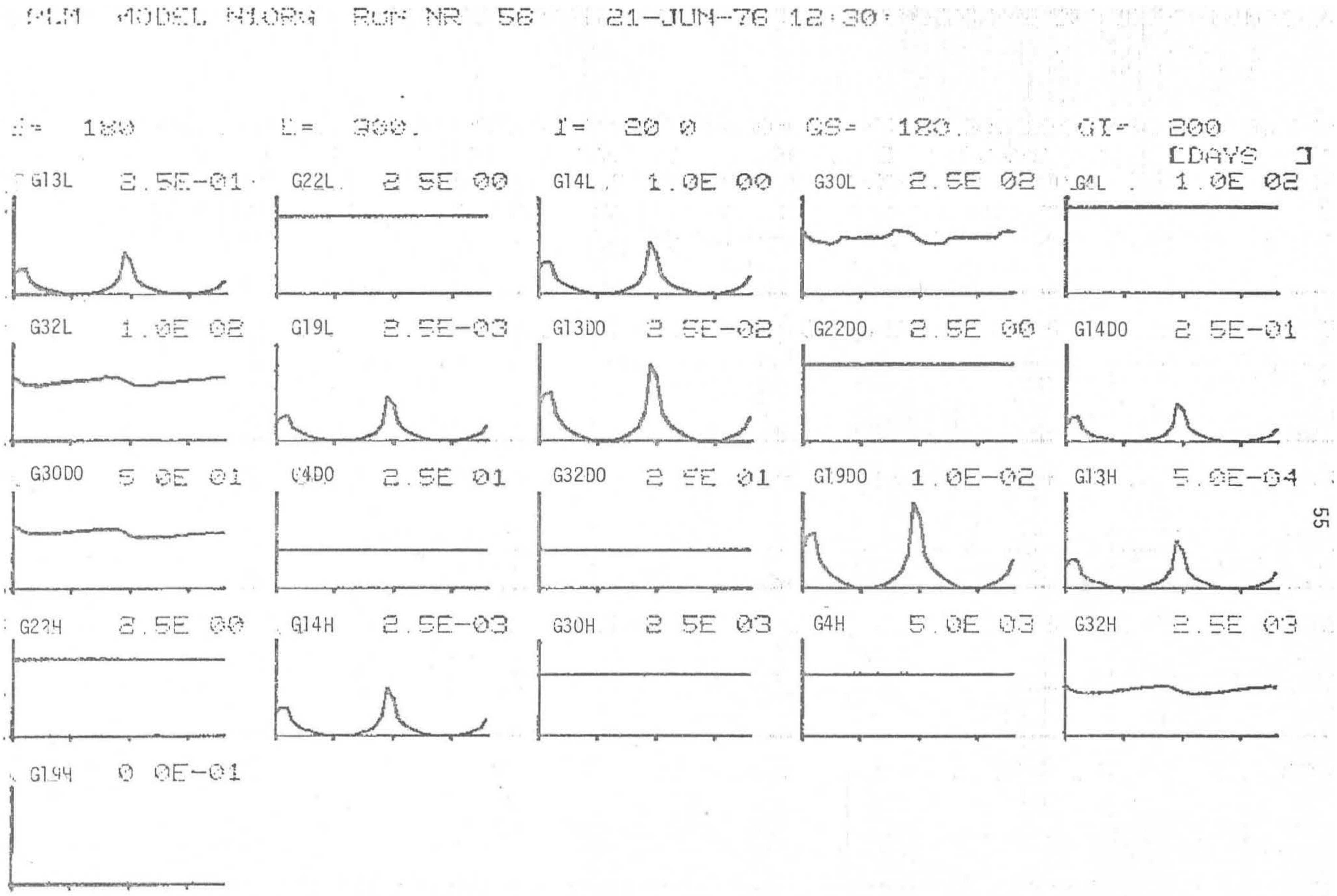


Fig. 5-c Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

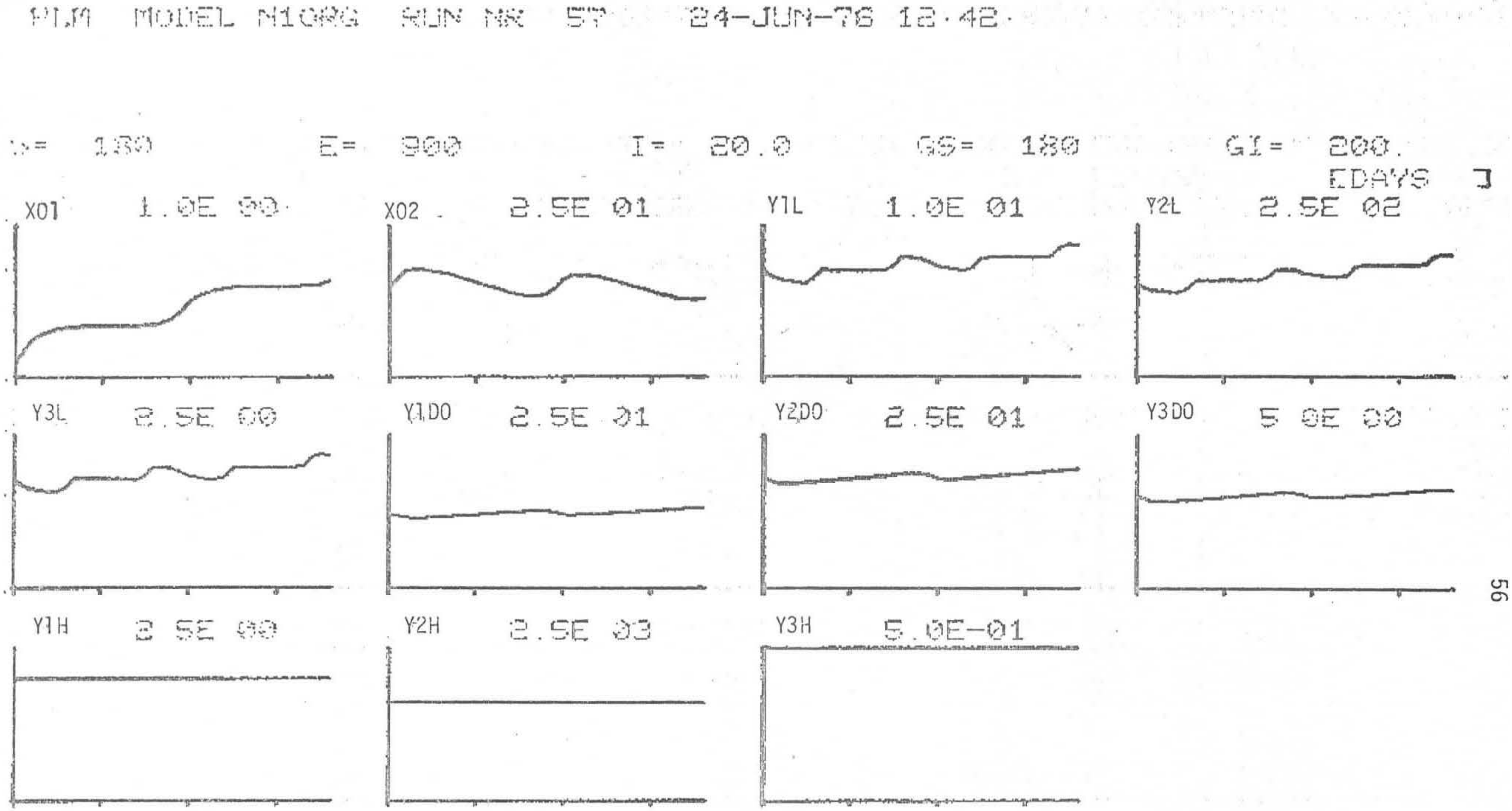


Fig. 6-a Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

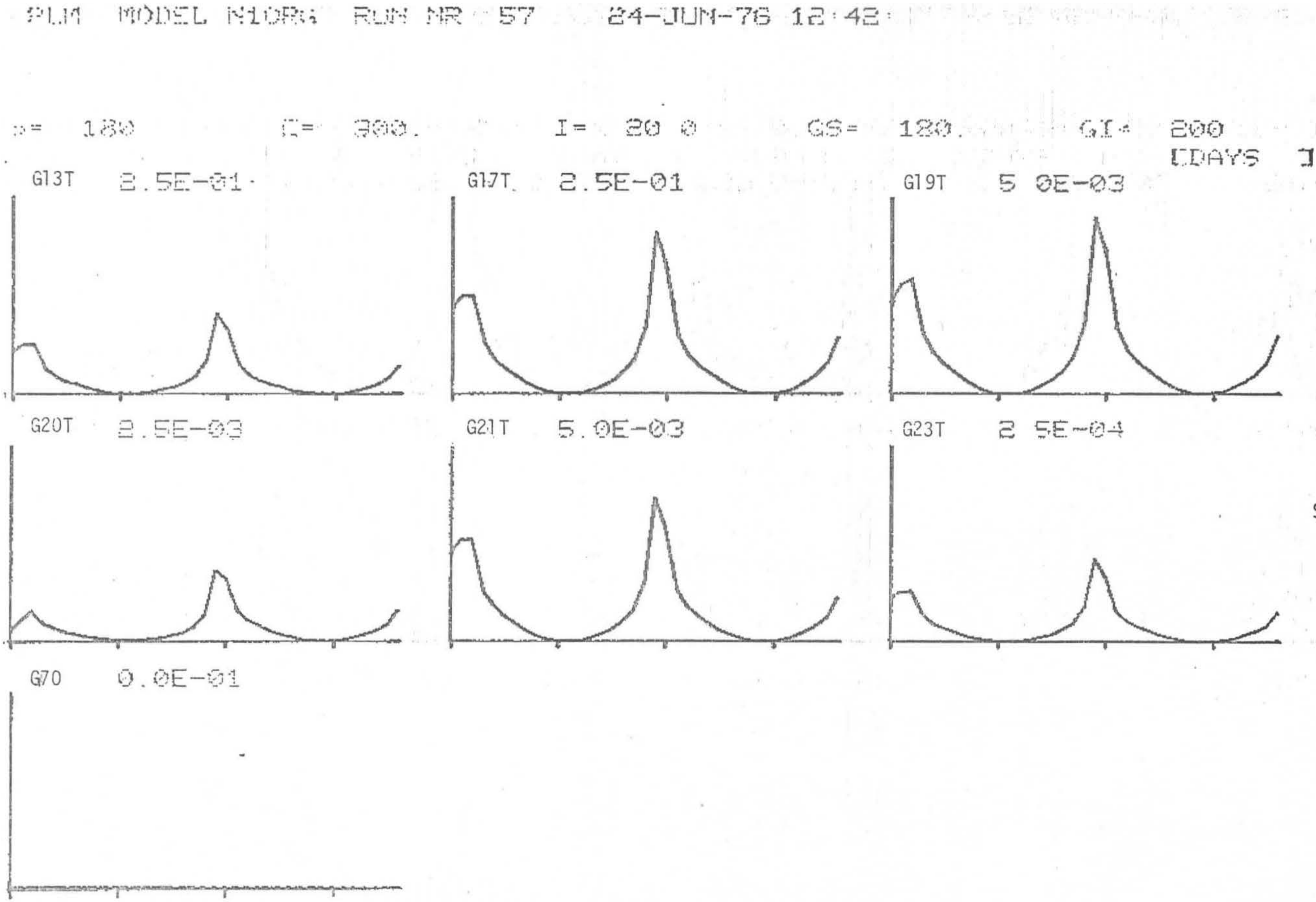


Fig. 6-b Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

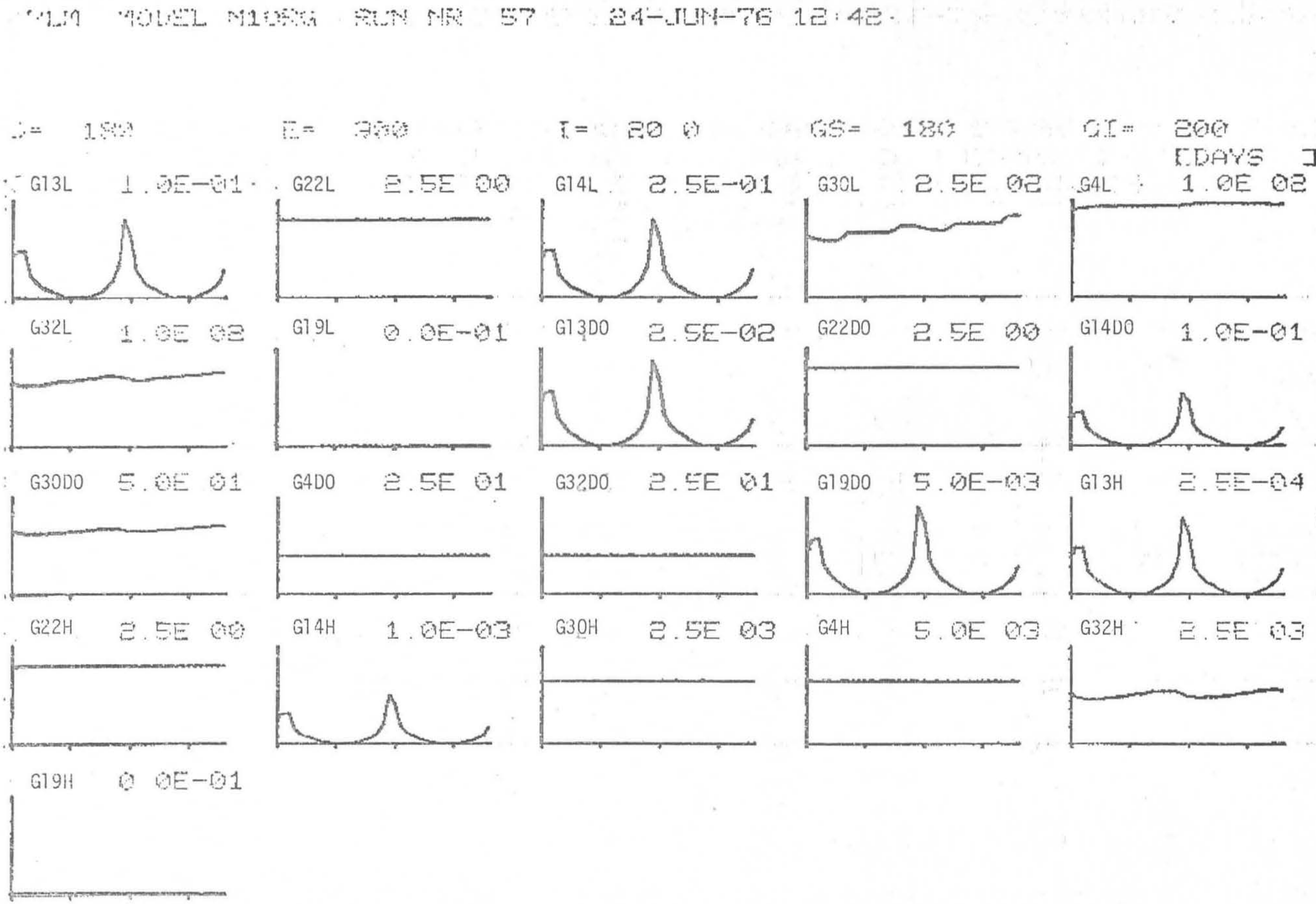


Fig. 6-c Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

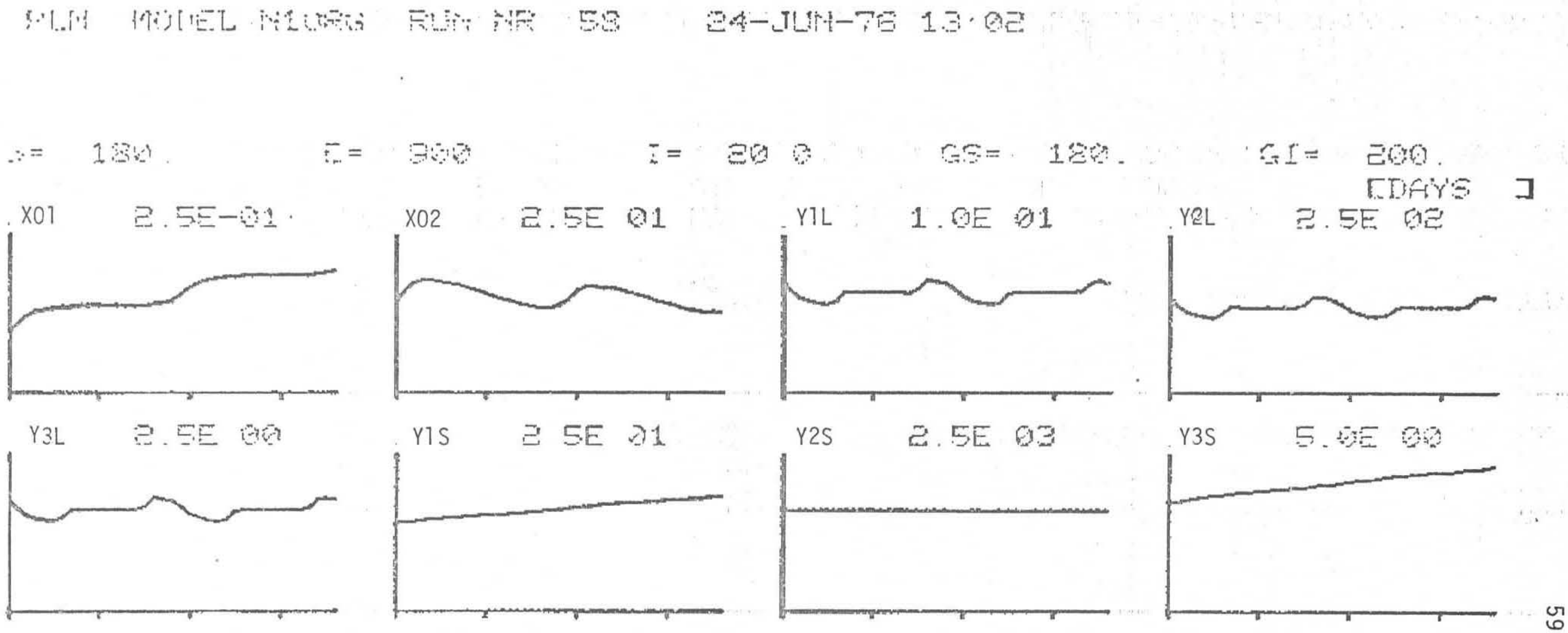


Fig. 7-a. Compartments with HUMUS and D.O. combined into SOM (S). The other variables are defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

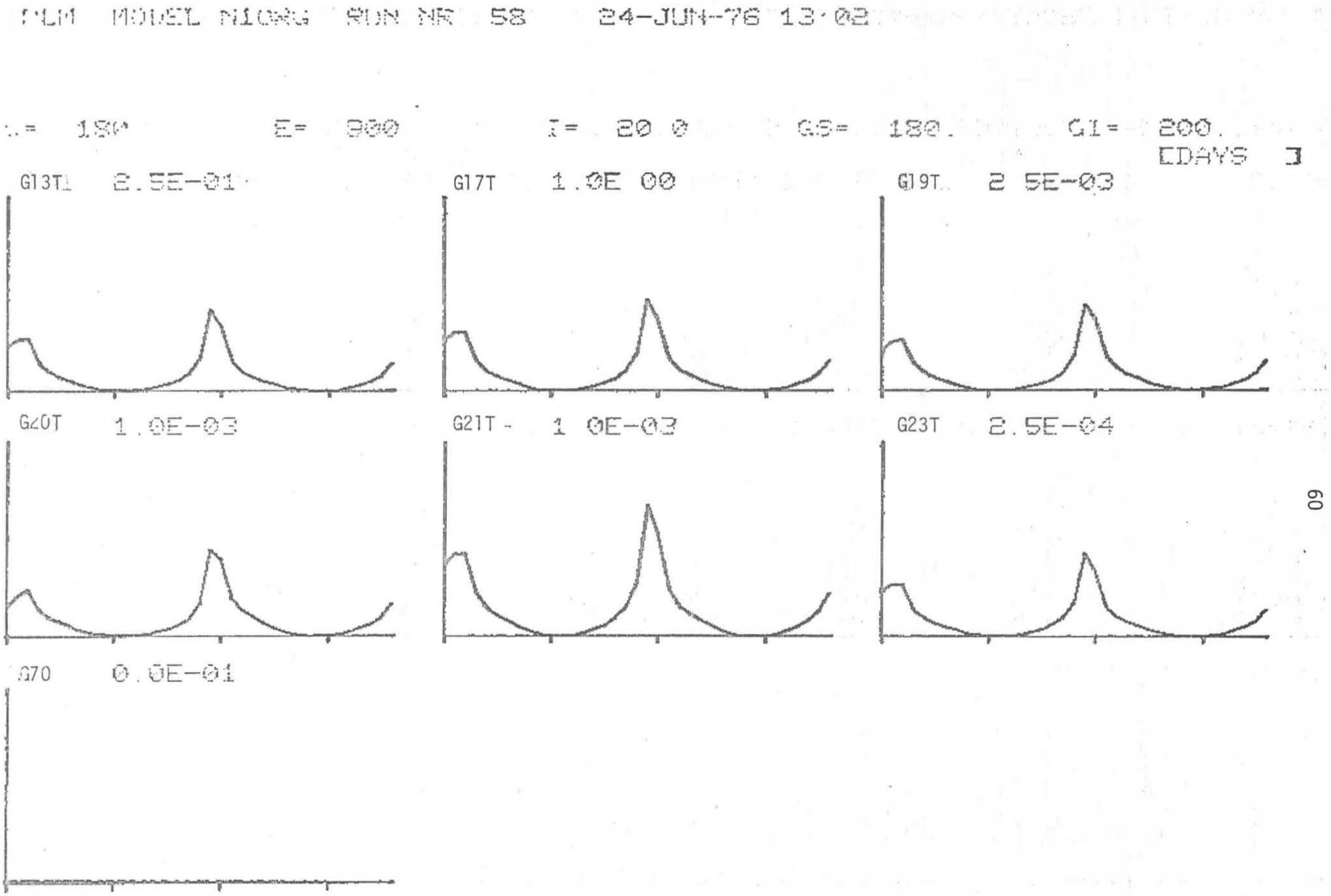


Fig. 7-b Variables defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.

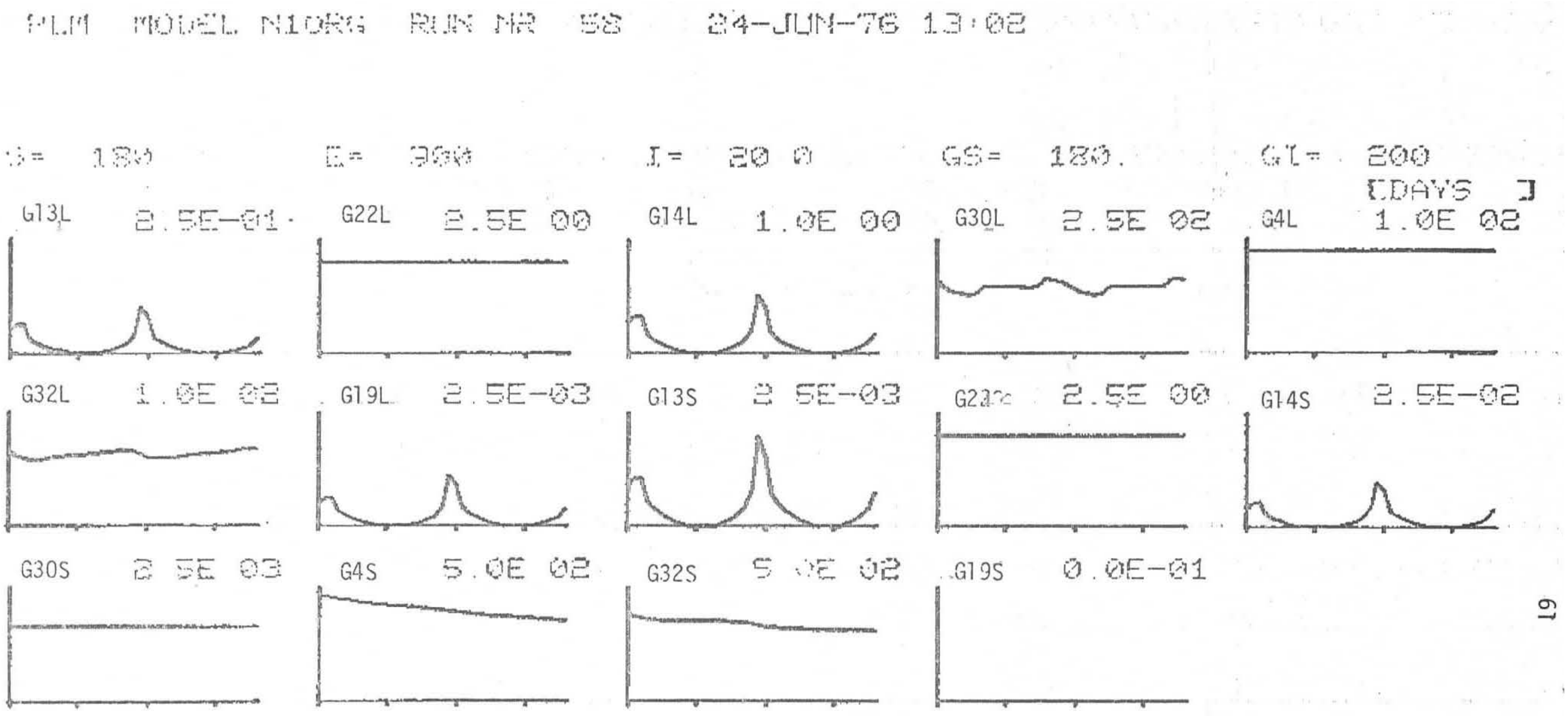


Fig. 7-c. G-functions with HUMUS and DO combined SOM (S). The other variables are defined in legends. Figure to the right of the variable symbol gives the value of the variable at the top of the axis. Time starts at July 1 of a year and ends two years later; each step on the time axis represents 200 days.